Effects of a Long Daily Photoperiod on Milk Yield and Circulating Concentrations of Insulin-Like Growth Factor-I

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ABSTRACT

Relative to a short daily (24-h) photoperiod, exposure to a long daily photoperiod increases the milk yield of dairy cows. However, the endocrine basis for this phenomenon is unknown. The present study was designed to test the hypothesis that a long daily photoperiod is associated with increased circulating insulin-like growth factor (IGF)-I, a hormone that is galactopoietic in ruminants. Forty lactating cows were exposed to either a natural photoperiod (≤13 h of light/d) or to a long daily photoperiod (18 h of light and 6 h of darkness) between January and April 1995. Cows were fed for ad libitum intake a total mixed diet formulated to meet the nutritional demands of lactation. Milk yield and dry matter intake were quantitated each day, and blood samples were collected by coccygeal venipuncture every 14 d. Plasma was harvested and assayed for IGF-I. The long photoperiod increased milk yield relative to the natural photoperiod (36.1 ± 0.6 vs. 33.9 ± 0.6 kg/d); the increase became significant after 28 d of treatment and was maintained for the duration of the study. In addition, cows exposed to a long photoperiod had greater circulating concentrations of IGF-I than did cows exposed to the ambient natural photoperiod (60.1 ± 2.0 vs. 52.6 ± 2.0 ng/ml). Concentrations of IGF binding protein-2 and -3 in plasma did not differ between treatments. These results support the hypothesis that a long daily photoperiod increases circulating concentrations of IGF-I in lactating cows and reveal a possible endocrine mechanism for the galactopoietic response to a long daily photoperiod.

(Key words: photoperiod, insulin-like growth factor-I, milk yield)

Abbreviation key: IGFBP = IGF binding protein, ST = somatotropin.

INTRODUCTION

First reported by Peters et al. (11), the galactopoietic response of cows to a long daily (24-h) photoperiod (16 to 18 h of light to 6 to 8 h of darkness) has subsequently been confirmed by a number of investigators (3, 6, 18). However, the physiologic explanation for this phenomenon is unknown. For example, the galactopoietic effects of somatotropin (ST) in cows are well characterized (2, 4), but there is no effect of a long photoperiod on the secretion of ST in cows (12). In contrast, long photoperiods are associated with increased circulating prolactin in cows (12). Treatment with exogenous prolactin, however, does not affect the milk yield of cows (13). Thus, the endocrine mechanism that mediates the increase in milk yield of cows that are exposed to long photoperiods has remained elusive.

Recent studies describing the response of cows and other ruminants to photoperiod, and specifically the stimulatory effect of long photoperiods on circulating concentrations of IGF-I, led us to hypothesize that long photoperiods stimulate IGF-I secretion in lactating cows and that this stimulation provides an endocrine signal for increased milk yield. This hypothesis was prompted by several observations. First, elevations in circulating and mammary immunoreactive IGF-I are associated with increased circulating prolactin in cows following treatment with exogenous ST (2, 4, 8). Second, long photoperiods stimulate IGF-I secretion in a number of species, including cattle, and these increases can be independent of ST (17, 19). Third, close arterial infusion of IGF-I in the mammary gland stimulates milk yield in goats, suggesting that the galactopoietic action of IGF-I is direct (14). To test our hypothesis that the increased milk yield of cows that are exposed to long photoperiods is mediated by increased circulating concentrations of IGF-I, we monitored the response of milk yield and plasma IGF-
Cows were housed in a tie-stall barn that was modified to control light exposure. Tie stalls were enclosed by curtains. Supplemental lighting (350 lx at eye level) was provided to cows under the long photoperiod treatment by metal halide lamps mounted at a height of 3.0 m. Lights were controlled by an automatic timer; they came on at 0530 h and shut off at 2330 h. Cows were tied in stalls and milked at 0600 and 1530 h. Milk yield was totaled daily and sampled once weekly (a.m. and p.m. samples) for composition analysis. Fat, protein, and somatic cell counts of milk were measured by automated infrared analysis (Fossomatic; Bentley Instruments, Chaska, MN) at the Mid-East DHIA (Hagerstown, MD). Yield of FCM was calculated according to the procedure of Tyrrell and Reid (20). A total mixed diet (Table 1) was fed for ad libitum intake once daily at 0900 h. The total mixed diet was formulated to provide adequate nutrition for a 635-kg cow yielding 43.1 kg/d of 3.5% FCM and assuming an intake of 22.1 kg/d of DM (10). Weight of the orts was recorded once daily just before new feed was offered. Cows were weighed at 1300 h for 2 consecutive d every 14 d beginning 2 d before photoperiodic treatments were imposed.

Blood Sampling and Analysis

Blood was sampled into tubes that contained heparin (16 × 100 mm; Vacutainer® No. 366480; B-D, Franklin Lakes, NJ) every 14 d at 0800 h by puncture of a coccygeal vessel using a 20-gauge ×
TABLE 2. Analysis of covariance for milk yield during the experimental period. 1

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>df</th>
<th>Description of source of variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>Fixed effect of light treatment</td>
</tr>
<tr>
<td>Pretreatment milk yield</td>
<td>1</td>
<td>Fixed regression effect of pretreatment milk yield on milk yield</td>
</tr>
<tr>
<td>Cow within treatment</td>
<td>35</td>
<td>Random variation among cows within treatment</td>
</tr>
<tr>
<td>Time</td>
<td>5</td>
<td>Fixed effects of biweekly time periods</td>
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<tr>
<td>Interaction of time and treatment</td>
<td>5</td>
<td>Fixed effects of interaction of time and treatment</td>
</tr>
<tr>
<td>IGF-I</td>
<td>1</td>
<td>Fixed regression effect of circulating concentrations of IGF-I on milk yield</td>
</tr>
<tr>
<td>Interaction of IGF-I and treatment</td>
<td>1</td>
<td>Fixed regression effect of interaction of circulating concentrations of IGF-I and treatment</td>
</tr>
<tr>
<td>Residual</td>
<td>163</td>
<td>Random variation among time periods within cow</td>
</tr>
</tbody>
</table>

1. The IGF-I and interaction of IGF-I and treatment was included to examine the relationship between IGF-I and milk yield and to compare the relationship between the two treatment groups. The same model was used to examine the relationship between milk yield and somatotropin, IGF binding protein (IGFBP)-2, or IGFBP-3 by replacing IGF-I with one of these three variables.

3.8-cm needle (B-D). Blood samples were stored at 4°C for a maximum of 1 h during collection. Plasma was harvested after centrifugation for 25 min at 1850 x g and frozen at -20°C until concentrations of IGF-I and ST were determined using previously validated radioimmunoassays (5). Sensitivity and intraassay and interassay coefficients of variation averaged, respectively, 2.0 ng/ml and 7.2 and 10.4% for IGF-I (two assays) and 1.2 ng/ml and 7.2 and 15.6% for ST (five assays).

The IGF binding proteins (IGFBP)-2 and IGFBP-3 were quantified using Western ligand blotting. Briefly, aliquots (10 μl) of plasma were separated electrophoretically using 12.5% SDS-PAGE, transferred to nitrocellulose paper, and probed with [125I]IGF-I. Molecular mass standards were run concurrently and were used to identify the migration of IGFBP-2 and IGFBP-3. Radioactivity in the resolved band was quantified using phosphoimaging technology and analysis on a Molecular Dynamics PhosphoImager (Molecular Dynamics, Sunnyvale, CA).

Statistical Analysis

The experiment had eight periods: one pretreatment period (d ±14 to ±1), six treatment periods (d 0 to 13, 14 to 27, 28 to 41, 42 to 55, 56 to 69, and 70 to 83), and one posttreatment period (d 84 to 97). All data were analyzed using an analysis of covariance model for a split plot in time (7). Repeated measures were analyzed with the compound symmetry variance-covariance structure in PROC MIXED of SAS (16). In all cases, the pretreatment value for that variable was used as a covariate in the model. Interactions of pretreatment and treatment and of pretreatment and time were included in the initial analysis but were dropped from subsequent analyses because they were not significant. A representative final model for the analyses is presented in Table 2. All ANOVA were covariant adjusted for pretreatment values; therefore, adjusted treatment means (least squares means) are reported. Correlations among cows were computed between the changes (mean across treatment periods minus pretreatment) in milk yield with the changes observed for each of the other variables (IGF-I, ST, IGFBP-2, and IGFBP-3). One cow under the natural photoperiod treatment was removed from the study after an injury, and data for that cow were not included in the analysis.

RESULTS

Milk Yield, Feed Intake, and Body Weight

Exposure of cows to a long photoperiod increased (P < 0.05) milk yield relative to that of cows exposed to the natural photoperiod (Figure 2). This stimulation of milk yield became significant after 28 d of the long photoperiod and was maintained throughout the treatment. During the posttreatment period, milk yield remained elevated in cows that had been exposed to the long photoperiod relative to those that had not received the extended light treatment. There was no effect of photoperiod on the percentage of fat [3.80% vs. 3.84% (±0.07%); P = 0.65], protein [3.40% vs. 3.38% (±0.02%); P = 0.47], or somatic cell count [202 × 10^3 vs. 332 × 10^3 cells/ml (±83 × 10^3 cells/ml); P = 0.17]. Because there was no effect on fat content in milk, data on FCM yields paralleled those on actual milk yield; mean FCM yield during treatment was 37.8 and 36.0 kg/d (±0.7 kg/d) for cows under the long and natural photoperiod treatments, respectively. Dry matter intake did not differ (P = 0.65) between treatments, averaging 23.1 and 22.8 kg/d (±0.4 kg/d) for cows under the long and natural photoperiod treatments, respectively. Body weight
EFFECTS OF LONG PHOTOPERIOD

Figure 2. Group means for milk yield of cows exposed to long (◊; 18 h/d) or natural winter (●; ≤13 h/d) photoperiods. Each symbol represents the mean yield of the cows (n = 20, long; n = 19, natural) within that group for the 14-d period. The hatched bar indicates the treatment period. Asterisks indicate differences between groups (*P < 0.05). Standard error of the difference (SED) for comparison between groups is indicated by the bar.

Figure 3. Group means for circulating concentrations of IGF-I of cows exposed to long (◊; 18 h/d) or natural winter (●; ≤13 h/d) photoperiods. Each symbol represents the mean of cows (n = 20, long; n = 19, natural) within that group for the single sample collected on the final day of each 14-d period. The hatched bar indicates the treatment period. Asterisks indicate differences between groups (*P < 0.05; **P < 0.02). Standard error of the difference (SED) for comparison between groups is indicated by the bar.

was not affected (P = 0.46) by treatment and averaged 631.4 kg (±1.2 kg) throughout the study.

IGF-I, IGFBP, and ST

Extension of the photoperiod from ≤13 h/d to 18 h/d of light increased (P < 0.05) mean plasma concentrations of IGF-I (Figure 3). This increase in IGF-I was temporally related to the increase in milk yield and became apparent at 14 d of treatment. Thereafter, circulating IGF-I remained elevated in cows exposed to long photoperiods. The correlations between IGF-I and change in milk yield were 0.20 (P = 0.41) and 0.05 (P = 0.82) for long and natural photoperiods, respectively. No difference was detected in circulating concentrations of IGFBP-2 (P = 0.24) or IGFBP-3 (P = 0.30) between groups at period 1, 4, or 7; pooled means within each group are presented in Figure 4. Between groups, there was no difference (P = 0.86) in plasma concentrations of ST at any period. Treatment means were pooled and averaged 4.4 ± 0.6 and 4.3 ± 0.6 ng/ml for cows under the long and natural photoperiod treatments, respectively. As with IGF-I, there were no significant correlations between change in milk yield and ST, IGFBP-2, or IGFBP-3.

DISCUSSION

The observation that cows exposed to the long photoperiod had increased milk yield relative to cows exposed to the natural winter photoperiod confirmed previous reports that long days are galactopoietic in cows (3, 6, 11, 18). Our finding that an increase in circulating concentrations of IGF-I accompanies the milk yield response to the long photoperiod extends those previous studies and provides support for the hypothesis that increases in IGF-I stimulate milk secretion even in the absence of increased ST. Further, the lack of an effect of the long photoperiod on IGFBP-2 or IGFBP-3 suggests that the influence of photoperiod is at the level of IGF-I secretion rather than the consequence of altered clearance or degradation.

Influences of photoperiod on IGF-I have been observed previously in a number of species, and there is evidence that the circadian pattern of melatonin secretion mediates these responses (17, 19, 21). For
example, long photoperiods increased circulating IGF-I in reindeer (19) and cattle (17) relative to short photoperiods. Melatonin treatment that mimics a short-day photoperiod increases IGF-I in hamsters (21). However, these seemingly divergent responses in effects of photoperiod on IGF-I across species are consistent with the inverted relationship between photoperiod and reproductive activity among short day breeders (e.g., sheep and reindeer) and long day breeders (e.g., hamsters). Thus, the response of IGF-I to long photoperiods in cows provides further support for the premise that melatonin acts as a timing signal, and various species have coopted that signal during evolution to provide control of endocrine systems involved in growth, reproduction, and, now, lactation.

Although consistent with previous reports (12, 17, 22), the lack of an effect of the long photoperiod on circulating concentrations of ST in the present study must be interpreted with some caution. Because of the pulsatile nature of ST release, subtle changes in the pattern of ST release would have been missed with the sampling scheme used (i.e., once every 14 d). However, cows at this age and stage of lactation have quite low, invariant secretion of ST (4). In addition, a sampling regimen that is similar to that employed in the present study has been used to evaluate changes in ST over longer time intervals, such as those occurring over the course of a lactation (15). Also, photoperiod does not affect ST clearance in cattle (22). Collectively, the present results and those of previous reports (12, 17, 22) support the conclusion that the long photoperiod does not affect circulating ST.

Because alterations of circulating IGF-I are often coincident with changes in ST, it is of interest to consider the mechanism whereby a long photoperiod increases IGF-I in the absence of any response of ST. One possibility is a shift in the balance of IGFBP that would cause a change in degradation or clearance of IGF-I (9). Although not an exhaustive examination of the IGFBP, the results for IGFBP-2 and IGFBP-3 in the present study did not support this premise. Rather, the present results suggest that the influence of photoperiod is at the level of IGF-I secretion. Possibly, a long photoperiod increases the responsiveness to ST at peripheral tissues such as the liver. Such a response would be consistent with the effects of photoperiodically induced secretory patterns of melatonin in the reproductive systems of some species, wherein melatonin may exert both gonadal and neuroendocrine actions.

The effect of a long photoperiod on IGF-I in the cow must also be considered in the context of the biological outcome, that is, increased milk yield. Bauman and Vernon (2) have suggested that the galactopoietic effects of ST in ruminants are mediated by the concomitant increases in circulating concentrations of IGF-I. Indeed, there is evidence that IGF-I has a direct galactopoietic action at the mammary gland (14), even in the absence of elevated concentrations of ST. In contrast, however, is the observation that circulating concentrations of IGF-I are inversely related to milk yield over the course of a lactation. That is, IGF-I is low at the start of lactation and increases to peak at the end of lactation (1, 15). The increase in IGF-I could possibly be modified by concurrent alterations in IGFBP, and, thus, the activity of the IGF system at the mammary gland may not always be reflected by changes in circulating concentrations of IGF-I alone. Because IGFBP-2 and IGFBP-3 were unaffected by the long photoperiod, the results of the present study support the concept that net increases in IGF-I are galactopoietic.

In conclusion, these data confirm the observation that a long photoperiod increases milk yield of lactating cows. This increase in milk yield is associated with a significant increase in circulating IGF-I that is independent of changes in ST, IGFBP-2, or IGFBP-3. Increased IGF-I represents a possible endocrine
mechanism for the galactopoietic effects of long photoperiods.

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REFERENCES


