

Photoperiodic Effects on Dairy Cattle: A Review¹

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ABSTRACT

Since the initial report in 1978 of galactopoietic effects of a photoperiod of 16 h of light:8 h of darkness, numerous studies have confirmed long-day stimulation of milk yield. The endocrine factor(s) responsible for increased milk yield, however, has eluded identification. Recent studies suggest that insulin-like growth factor-I (IGF-I) may mediate the galactopoietic response to long day photoperiod. Indeed, long days increase IGF-I in heifers and lactating cows; in the latter case, the response preceded an increase in milk yield. In heifers and cows, the increase in IGF-I is independent of changes in circulating growth hormone. Melatonin feeding to mimic a short-day photoperiod suppressed the increase of IGF-I in heifers induced by long days. However, melatonin feeding had no effect on milk yield in cows. Despite lack of resolution of the endocrine mechanism, dairy producers are interested in how photoperiod management can be integrated with current practices throughout the lactation cycle. There is strong evidence that milk yield responses to long days persist through an entire lactation. Also, long days can be combined with bovine somatotropin (bST) to produce additive increases in milk yield. During the dry period, long days increase the periparturient surge of prolactin. However, relative to long days, short-day treatment during the dry period produces the largest magnitude of response in milk yield during the subsequent lactation. The response to short days during the dry period may be due to a priming effect on the photoperiodic response system. In summary, IGF-I has emerged as a possible mediator of the increase of milk yield in response to long-day photoperiod. Photoperiod can be combined effectively with other management techniques such as bST. Consideration of photoperiod management during

the dry period is essential to maximize responses during the subsequent lactation.

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

Abbreviation key: GH = growth hormone, IGFBP = insulin-like growth factor binding protein, PRL = prolactin.

INTRODUCTION

A number of management tools are available to dairy producers, which serve to increase milk production during an established lactation. These include bST, milking more than twice daily (i.e., 3×), and the subject of this review, manipulation of photoperiod. Increased photoperiod has long been used to enhance growth and production in domestic species. With regard to lactation, increasing light exposure from less than 12 h of light/d (short-day photoperiod) to 16 to 18 h of light/d (long-day photoperiod) enhances milk production an average of 2.5 kg/cow per d. The endocrine mechanism that underlies these effects, however, has eluded characterization. Further, integration of photoperiod into the management scheme for an entire lactation cycle has not been fully developed.

Recently, a series of experiments has produced evidence that long-day photoperiod may be acting via increases in circulating IGF-I. In addition, we have begun to describe a framework of recommendations for the use of photoperiod during the entire lactation cycle, including the dry period. Collectively, these experiments provide strong support for the use of photoperiod as an effective, noninvasive method to enhance milk production in cattle.

Photoperiodic Perception and Signal Transduction

It is best to begin with a brief review of the mechanisms of photoperiodic signal perception and transmission. In cows and other mammals, photoperception occurs at the retina, and cattle appear to be able to discriminate light at intensities as low as 5 lx (35). Light impinging on the eye stimulates retinal photoreceptors that transmit an inhibitory signal to the pineal gland through a series of interneurons via the retino-hypo-

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thalamic tract [reviewed in (41)]. The pineal secretes a number of hormones, but the indoleamine melatonin is generally accepted as the active mediator of photoperiodic responses (40, 41). Light inhibits activity of the rate-limiting enzyme in melatonin synthesis, N-acetyltransferase (18). Thus, secretion of melatonin from the pineal gland would be low during light exposure, so concentrations during the photophase hover around assay sensitivity (5, 17). When lights are off, the inhibition is removed, and melatonin secretion rapidly increases, such that elevated concentrations of melatonin are present in the scotophase or dark period. One critical feature of photoperiodic responses is the requirement of a dark phase for the responsiveness to persist. In the absence of any scotophase, for example, in a continuous lighting regime, animals lose the ability to track daylength and circadian events lose synchronicity or free-run (5, 56). Based on a limited number of studies, it appears that free-running cows default to short-day photoperiodic responses, and therefore continuous lighting is not recommended (5, 25).

In cattle, as in other species, there is dependence on the pineal for photoperiodic responses. Indeed, blinding and pinealectomy eliminate rhythmic patterns of melatonin release and, thus, photoperiodic responses (31). Coding for daylength, therefore, depends on the duration of elevated melatonin secretion. That is, the length of the period that melatonin secretion is elevated determines relative daylength to the animal through synchronization of the endogenous circadian rhythm. An endogenous circadian rhythm sets a relative dawn, and animals then track photoperiod to determine daylength relative to that subjective dawn (41, 56). If light is perceived (i.e., low melatonin) approximately 15 h after dawn, a time termed the photosensitive phase, that is the cue for a long day. In contrast, the presence of darkness (i.e., high melatonin) during the photosensitive phase will be perceived as a short day. This photosensitivity can be exploited with a skeletal photoperiod such that, following dawn, cows can be exposed to darkness until the photosensitive phase and then exposed to light between 14 and 16 h after subjective dawn. Such a skeletal photoperiod has been used successfully to elicit long-day photoperiodic responses in cattle (11). The melatonin pattern thus influences secretion of a number of hormones, and it is the endocrine effects of photoperiod that result in physiological alterations in growth, reproduction, and lactation.

Photoperiodic Effects on Reproduction and Growth

Light manipulation has been used to increase productivity of livestock for many years. Chickens are exposed to long days to increase production of eggs (59). For

seasonal breeders such as sheep and horses, entry and egress from the breeding season can be timed through appropriate manipulation of photoperiod (13, 47). Indeed, the effects of photoperiod on reproduction is well characterized for many species (40). Although cattle are not seasonal breeders in the strict sense of distinct seasons of reproductive activity and inactivity, there is evidence of seasonal bias in bovine reproduction. For example, return to estrous cyclicity is longer in cows that calve in winter relative to those calving in the summer [reviewed in (14)]. Timing of puberty is also influenced by season of birth (45). Although various environmental and management factors vary with season, the effects observed on reproduction in cattle are heavily influenced by the prevailing photoperiodic conditions. A number of laboratories have observed that heifers exposed to long days achieved puberty earlier than herdmates exposed to short days (16, 25, 45). In sheep, photoperiodically induced changes in reproductive neuroendocrine activity result from alterations in the responsiveness to estradiol negative feedback (43). Consistent with that is the observation that cattle exposed to 18 h of light:6 h of darkness had greater luteinizing hormone response to estradiol than those heifers on 8 h of light:16 h of darkness (15).

At least a portion of the effect of photoperiod on reproduction may be explained via body growth and compositional changes. Long days increase growth rates in cattle, as well as hastening onset of puberty (16, 25). In prepubertal animals, enhanced growth is associated with decreases in protein turnover (63), and the animals have greater feed efficiency (25, 29). Postpubertal animals increase accumulation of fat when treated with short days (63). Of interest, heifers and steers on long days do not spend more time eating (33, 61), nor do they rapidly increase DMI in response to longer days and, thus, stimulate gain (23, 29). Rather, it appears that increases in DMI in growing animals exposed to long days lag the stimulation of growth.

With regard to mammary growth, long days increase parenchymal tissue and limit fat in heifers relative to animals on short days (30). Further, feeding of melatonin in the middle of the scotophase to mimic a short-day pattern elicits similar responses of mammary growth and fat accumulation to those observed with short days (44, 62). Because many studies have revealed effects of photoperiod on nutrient partitioning (i.e., increased feed efficiency and lean gain) and the endocrine system [i.e., increased prolactin (PRL) secretion], it is perhaps not surprising that there would be a galactopoietic action of long days as well.

Photoperiodic Effects on Lactation

Observation that long-day photoperiod increased circulating PRL in a number of species prompted investi-

Table 1. Summary of studies reporting effects of supplemental lighting on milk yield in lactating cows.

Authors (reference)	Location (latitude)	Light type	Responses to long days		
			Milk yield increase (kg/d)	Fat % ¹	DMI increase
Peters, et al. (27)	Michigan (42°N)	Fluorescent	2.0	NC	...
Peters, et al. (26)	Michigan (42°N)	Fluorescent	1.4	NC	6.1%
Marcek and Swanson (19)	Oregon (45°N)	Sodium vapor	1.8	Variable	...
Stanisiewski, et al. (52)	Michigan (42°N)	Fluorescent	2.2	0.16↓	...
Bilodeau, et al. (4)	Quebec (47°N)	Fluorescent	2.0	NC	4%
Evans and Hacker (11)	Ontario (43°N)	Fluorescent	2.8	NC	NC
Philips and Schofield (34)	Wales (53°N)	Fluorescent	3.3	0.18↓	NC
Dahl, et al. (9)	Maryland (39°N)	Metal halide	2.2	NC	NC
Reksen, et al. (39)	Norway (60–62°N)	Fluorescent	0.5	...	...
Miller, et al. (22)	Maryland (39°N)	Metal halide	1.9	NC	3.5%

¹NC = no change; arrow indicates direction of change.

gation of the effects of photoperiod on milk yield. Peters et al. (27) made the initial discovery that long days increased milk yield in cows relative to those exposed to an ambient photoperiod between September and April in Michigan. Subsequently, at least seven different laboratories across North America and Europe, in latitudes ranging from 39°N to 62°N, have confirmed that long-day photoperiod increases milk yield (Table 1). Indeed, a recent study by Reksen et al. (39) suggests that simply exposing cows to more than 12 h of light each day stimulates milk production relative to cows that receive less than 12 h of light/d. Milk composition is generally unaffected by photoperiod, although some studies indicate a slight depression of milk fat percentage may occur during exposure to long days [Table 1; (34, 52)]. Effects of long days on DMI in lactating cows are not always observed, but, generally, DMI increases in longer-term studies to meet the increased demand for energy output from the mammary gland (Table 1). Overwhelmingly, the evidence supports the concept that long days are galactopoietic in cattle. The endocrine mechanism underlying the response, however, is not understood.

Prolactin emerged as the initial candidate responsible for the galactopoietic effects of photoperiod. Indeed, long days increase circulating concentrations of PRL in a number of species, including cattle (28, 58). Short days, and melatonin replacement to mimic short days, decrease circulating PRL (6, 44, 48). Because of the galactopoietic role of PRL in a number of species, it would appear to be a logical mediator of the photoperiodic effect on lactation in cows. However, two critical observations argue against PRL causing the effects of long days on milk yield. First, provision of exogenous PRL has no effect on milk yield in cows, either before or after peak lactation (36). Those results, however, must be interpreted with caution in regard to photoperiodic effects, because the study terminated (i.e., 4 wk)

when long-day effects on milk yield typically become apparent. The second observation is perhaps more informative with regard to the role of PRL in photoperiodic responses. That is, increases in PRL induced by long days are overridden by temperatures below freezing (25). Yet, effects of long days persist at low temperatures (25, 52). Thus, although not yet tested directly, a role for PRL in mediating the effects of long days on milk yield is not supported by the evidence available.

A second hormone possibly related to the galactopoietic effects of long days is growth hormone (GH). It is well established that increased circulating concentrations of GH, either exogenously (3) or endogenously (7), increase milk yield in lactating cows. However, there is little evidence that photoperiod influences GH secretion in cattle. Photoperiod does not affect mean daily concentrations (28), characteristics of pulsatile release (63), or secretion and clearance rates of GH (61) in cattle. Nor does photoperiod influence stimulated responses to GH secretagogues. For example, there is no difference in the GH response to thyrotropin-releasing hormone between cows on long versus short days (26). Responsiveness to GH-releasing hormone was greater in calves exposed to long days relative to those on short days after 90 d of treatment, but the opposite was observed after 246 d of treatment (42). There is recent evidence (2) of a seasonal fluctuation of GH in cattle, but whether or not that is associated with photoperiodic changes was not determined. Collectively, a role for changes in GH secretion due to photoperiod causing the galactopoietic response to long days is not supported by experimental data. Other hormones within the somatotrophic axis, however, are affected by photoperiod. Namely, IGF-I concentrations fluctuate with photoperiodic treatment independent of GH and could possibly explain the effects of long days.

Photoperiodic Influences on IGF-I

Many reports suggest that seasonal changes in IGF-I, particularly those described in ruminants, are driven by annual differences in photoperiod. The substantial increase in growth of red deer in the spring is associated with elevated concentrations of IGF-I (54). In reindeer, a similar increase in circulating IGF-I, driven by a long-day photoperiod, significantly increases growth (55). Melatonin implants, which mimic a short-day photoperiodic signal, suppress IGF-I secretion in red deer (53). In contrast, Syrian hamsters display an increase in IGF-I with melatonin treatment that mimics short days (60). The apparent paradox with regard to long-day effects on IGF-I in some rodents relative to ruminants is consistent with the opposing responses of the gonadotropins to long days across these groups. That is, both use photoperiod to synchronize annual events such as growth and reproduction, yet these events are timed to occur in the geophysical year when other environmental factors (i.e., food availability and temperature) are most conducive to a successful outcome. Combined, the evidence strongly supports the hypothesis that long days stimulate secretion of IGF-I in ruminants and provide a possible endocrine mechanism by which photoperiod effects on growth might be explained.

Determination of the relationship of IGF-I to photoperiod in cattle was of interest to us, given the preceding discussion. To test the hypothesis that long days increased IGF-I, prepubertal heifers were exposed to 8 h of light:16 h of darkness for 4 mo (51). Blood samples collected monthly were assayed for IGF-I. Over the 4-mo period, heifers on 16 h of light:8 h of darkness had consistently greater circulating IGF-I relative to those on 8 h of light:16 h of darkness, supporting the hypothesis that long days increase IGF-I in cattle. To determine whether a short-day photoperiod would in turn negate the stimulatory effects of long days, we fed melatonin to prepubertal heifers in the middle of the photophase of a 16 h of light:8 h of darkness cycle and quantified IGF-I over 2 mo (49). There was no difference in IGF-I between control and melatonin fed heifers on d 1 of treatment. However, control heifers experienced an increase in IGF-I over the 2 mo, whereas the melatonin fed heifers had no change; melatonin feeding had no effect on circulating GH or IGF-binding protein (IGFBP)-2 or -3 (48). These data provide further support to the hypothesis that photoperiod influences IGF-I in cattle with that response being stimulated by long days and inhibited by short days.

The physiologic responses to long days in heifers are consistent with stimulation of IGF-I. For example, long days increase mammary parenchymal growth relative to short days (30), and IGF-I increases bovine mam-

mary growth in vitro (20, 46). Melatonin feeding to mimic short days is suppressive to mammary parenchymal growth (44). Compared with short days, long days increase lean tissue accretion and growth (58), both of which are associated with elevated concentrations of IGF-I (10). Photoperiodic control of IGF-I release, therefore, is consistent with the observed responses in carcass and mammary growth in cattle. The question becomes: What about lactation?

Endocrine Responses to Photoperiod and Melatonin in Lactating Cows

Although there is evidence that IGF-I is not galactopoietic in cows [reviewed in (57)], exogenous IGF-I elicits acute galactopoietic effects in goats (37, 38). In addition, Glimm et al. (12) observed that IGF-I binding to mammary epithelial cells increases in lactating cows treated with bST, which, in turn, is associated with increased milk yield. Because long-day photoperiod increases IGF-I in cattle, we designed an experiment to address the hypothesis that the galactopoietic effects of long days were associated with an increase in IGF-I secretion (9). Thirty-nine lactating cows were assigned to long-day photoperiod (18 h of light:6 h of darkness; $n = 19$) or ambient photoperiod (10 to 13 h of light:14 to 11 h of darkness; $n = 20$) for 12 wk. Milk yield was recorded daily, and blood samples were collected at 14-d intervals to quantify IGF-I, PRL, GH, IGFBP-2, and IGFBP-3 in plasma. Relative to ambient photoperiod, long days increased milk yield (Figure 1, Panel A), IGF-I (Figure 1, Panel B), and PRL. Of interest, significant divergence of circulating IGF-I appeared before the milk yield separated by treatment (Figure 1). There was no difference between groups in GH, IGFBP-2, or IGFBP-3, suggesting that the effect of long days on IGF-I was at the level of secretion rather than via altered IGF-I clearance or GH stimulation. These results support the working hypothesis that long day-induced increases in IGF-I may be driving the galactopoietic effect of long days.

A logical extension of the overall hypothesis that altered patterns of melatonin secretion between long and short days are driving photoperiodic effects is the expectation that melatonin feeding to mimic a short day would depress milk production. Indeed, melatonin feeding decreases mammary gland (44) and lean tissue growth in heifers (62), as well as suppressing PRL and IGF-I responses to long days (48). To test the hypothesis that melatonin feeding to mimic a short-day pattern of release would decrease milk yield during an established lactation, 26 cows were exposed to 18 h of light:6 h of darkness; 13 cows received a daily oral bolus of 22.5 mg melatonin in the middle of the photophase for 8

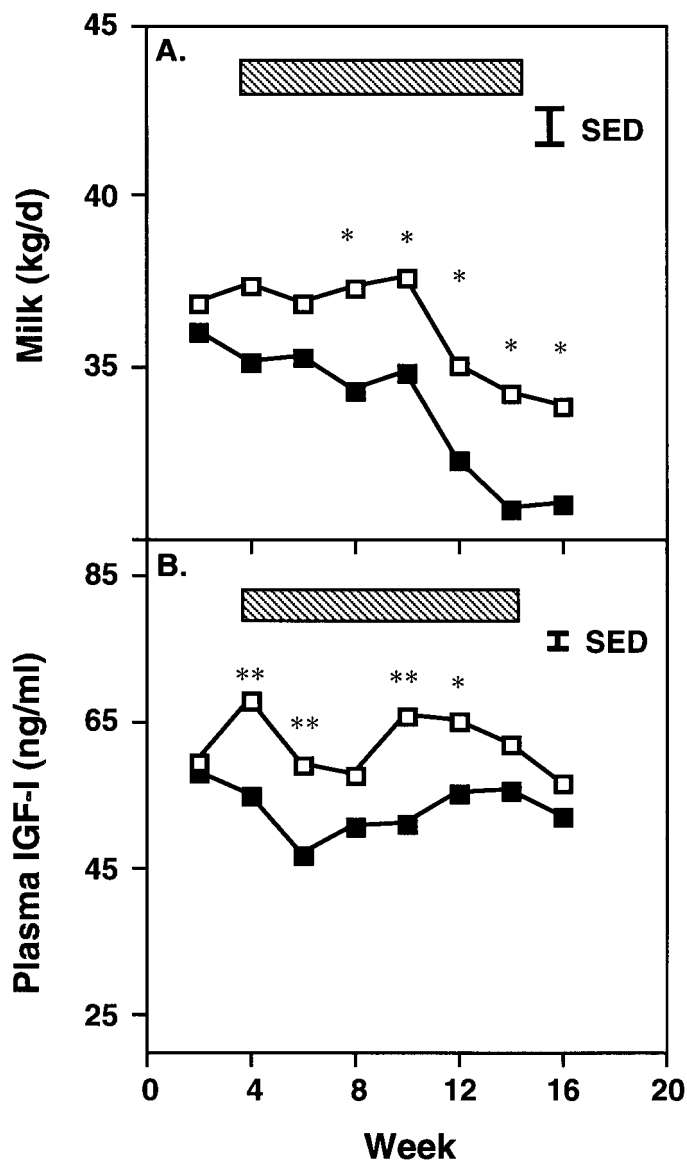


Figure 1. Group means for milk yield and circulating IGF-I of cows exposed to long-day (□) or natural (January to May in Maryland; ■) photoperiods. The hatched bar indicates the periods when photoperiodic treatment was imposed. Asterisks indicate differences between groups (* $P < 0.05$; ** $P < 0.02$). Standard errors of the difference (SED) for comparison between groups are indicated by the vertical bars. Panel A: Each symbol represents the mean milk yield of the cows (□, $n = 19$; ■, $n = 20$) within that group for the 2-wk period. Panel B: Each symbol represents the mean circulating IGF-I of the cows (□, $n = 19$; ■, $n = 20$) within that group for the single sample collected on the final day of each 2-wk period. Adapted from Dahl et al. (8).

wk. The remaining 13 cows received a vehicle bolus. Relative to controls, melatonin feeding suppressed serum PRL at 4 and 8 wk (Figure 2), suggesting that the cows responded to the melatonin regimen. Despite the PRL response, there was no difference in milk yield between groups (Figure 3). Because this study was con-

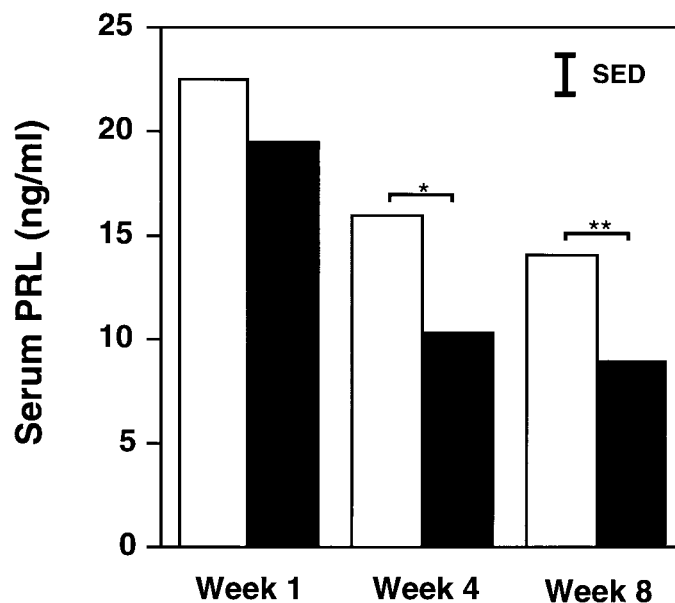


Figure 2. Group means for prolactin (PRL) of cows exposed for 8 wk to long-day photoperiod (open bars, $n = 6$) or long-day photoperiod and fed melatonin (solid bars, $n = 6$). Asterisks indicate differences between groups (** $P < 0.07$; * $P < 0.12$). Standard error of the difference (SED) for comparison between groups is indicated by the vertical bar.

ducted in late-lactation cows (average 217 ± 27 DIM) that were already in the declining phase of production, further depression of milk yield may have been masked. Thus, the experiment was repeated in early lactation cows [(6); 98 ± 18 DIM]. Again, melatonin feeding decreased serum PRL but had no effect on milk yield.

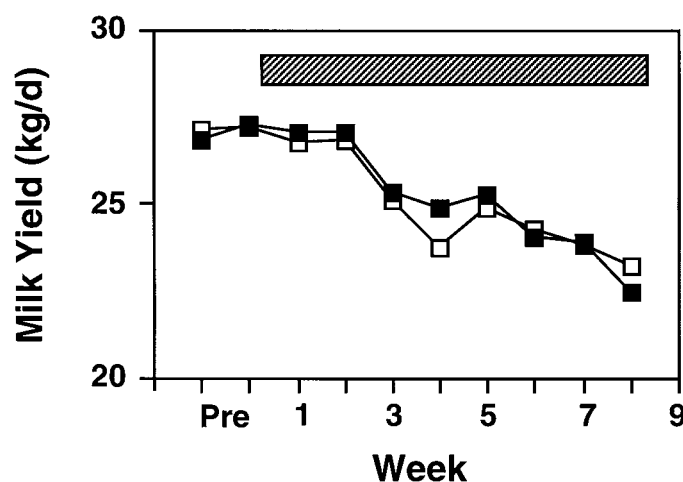


Figure 3. Group means for milk yield of cows exposed for 8 wk to long-day photoperiod (□, $n = 13$) or long-day photoperiod and fed melatonin (■, $n = 13$). The hatched bar indicates the periods when melatonin feeding was imposed. Milk yield did not differ at any time between groups ($P > 0.10$).

Table 2. Treatment means and standard errors of the difference (SED) for yield, fat corrected milk (FCM), protein percentage, and fat percentage for cows exposed to a long daily (LD) or a natural daily (ND) photoperiod (PP) with or without bST administration. Adapted from Miller et al. (22).

	NDPP ¹	LDPP	NDPP + bST	LDPP + bST	SED	P-value		
						bST	PP	bST × PP
Milk, kg/d	25.2	27.1	30.5	31.7	1.7	0.01	0.22	0.78
3.5% FCM, kg/d	27.7	29.6	33.4	35.4	1.6 ²	0.01	0.12	0.54
Protein, %	3.3	3.2	3.3	3.2	0.08	0.62	0.21	0.79
Fat, %	4.2	4.1	4.2	4.4	0.2	0.26	0.62	0.15

¹NDPP = 9.5 to 14.5 h of light and 14.5 to 9.5 h of darkness/d; LDPP = 18 h of light and 6 h of darkness/d.

²The SED for NDPP + bST = 2.4 because of heterogeneous variance.

Results from the two studies suggest that melatonin feeding in mature cows does not mimic the effect of short days on milk yield, although PRL effects are observed. This phenomenon is of interest to producers, particularly those in situations that may preclude establishment of a consistent 6- to 8-h period of darkness during each day (i.e., 3× milking). Unfortunately, feeding of melatonin is not an appropriate method to simulate darkness to cows on 24 h of light and, thereby, to elicit a long-day effect.

Combining Photoperiod with Other Management Techniques

To this point, the focus of this review has been the biological mechanisms that underlie photoperiodic responses. It is also of interest to consider photoperiod treatment in the context of other management practices, particularly the use of bST and treatment of the dry cow.

With regard to bST, a combination of bST with 3× milking produces additive galactopoietic effects (50). Because the effect of long days is independent of GH, we hypothesized that bST and long days would produce additive or synergistic stimulation of milk yield. We tested this hypothesis using 40 cows in a 2 × 2 factorial design of photoperiod and bST (22). Long days increased milk yield relative to ambient photoperiod, and this response became significant after 4 wk. Relative to vehicle-treated controls, bST increased milk yield. The combination of bST and long-day photoperiod caused an additive increase in milk yield [(22); Table 2]. Milk composition was not affected by bST or photoperiod, but component yields increased parallel to increases in milk yields. Thus, it is possible to use bST and long days together to achieve greater milk yield increases than with either alone.

Of interest, examination of DMI responses in our study revealed differences between photoperiod and bST with regard to the effects of increased yield on DMI

(Figure 4). That is, cows on long days met the increased nutrient demands for higher milk yield by increasing intake, whereas those on bST appeared to mobilize body reserves preferentially. This finding was consistent with the observation that bST, but not photoperiod, depressed energy balance. The combination of bST and long days increased intake earlier, despite the fact that milk yield did not diverge between the bST and bST plus long-day photoperiod cows until the latter part of the study. Thus, long days may be of benefit to stimulate intake in cows treated with bST.

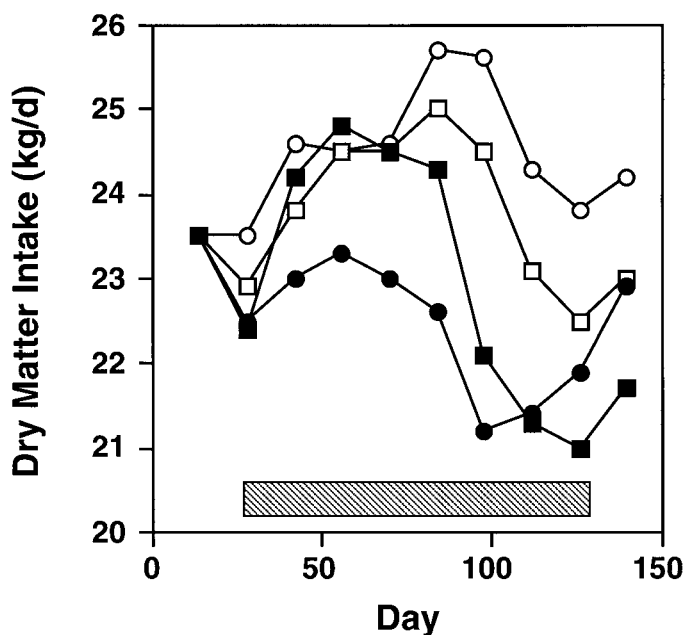


Figure 4. Group means for DMI of cows exposed to long-day (□, n = 10) or ambient (■, n = 10) photoperiods with or without bST administration (long days + bST = ○, n = 10; ambient + bST = ●; n = 9) by day of experiment (DAY). The hatched bar indicates the periods when photoperiodic and bST treatments were given. Each symbol represents the mean DMI of the cows within that group for the 14-d period. Standard error of the difference for comparison among groups = 0.6. Reprinted with permission from the *Journal of Dairy Science* (22).

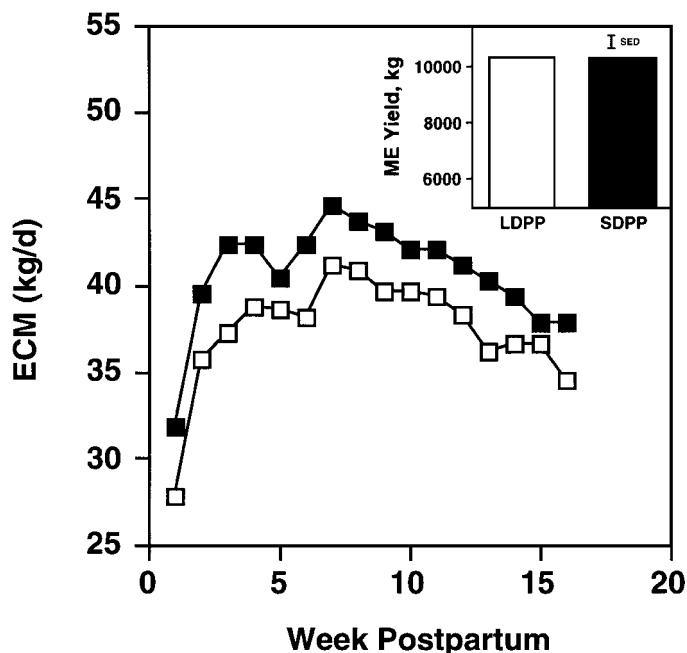


Figure 5. Group means for energy-corrected milk yield (ECM) during the subsequent lactation of cows exposed to long-day (LDPP = □; $n = 18$) or short-day photoperiods (SDPP = ■; $n = 16$) during the dry period. At calving all cows returned to natural photoperiodic conditions (January to June in Maryland). Each symbol represents the mean yield of the cows in that group for that week of lactation, through the first 16 wk of lactation. Yields were different between groups ($P < 0.07$). The inset depicts the average ME of milk (and standard error of the difference) for the previous lactation, confirming that the groups were uniform with regard to production potential. Adapted from Miller et al. (21).

In contrast to the lack of effect of PRL during an established lactation, a robust periparturient PRL surge is essential to complete lactogenesis at calving (1). We have previously observed (24) that long days during the final trimester increased the magnitude of the periparturient PRL surge in heifers. Based on those results, we hypothesized that a greater magnitude PRL surge would enhance production in the next lactation. Therefore, we exposed 34 cows to either 8 h of light:16 h of darkness or 16 h of light:8 h of darkness during the dry period to determine the effects on subsequent milk yield (21). At calving, all cows returned to the ambient photoperiodic conditions of the herd. Long days during the dry period caused a greater magnitude periparturient PRL surge relative to short days, confirming the work of Newbold et al. (24). In contrast, cows exposed to short days during the dry period produced an average of 3.1 kg more milk/d than those on long days (Figure 5), which, combined with the PRL data, suggests that increasing the magnitude of the PRL surge with photoperiod is without effect on subsequent yield of milk. Our results are consistent with a recent prelimi-

nary report by Petitclerc et al. (32) in which cows were treated with short days or long days or fed melatonin to mimic short days during the dry period. At calving, all cows were placed on long days for that lactation. Again, cows on short days during the dry period produced significantly more milk relative to those exposed to long days. The observed effect of short days during the dry period may be due to the fact that cows become refractory to a constant light pattern, and exposure to short days resets the responsiveness of a cow to the stimulatory signal. Fortunately, the dry period offers an ideal time to expose cows to a short-day photoperiod.

CONCLUSIONS AND IMPLICATIONS

Exposure to long days increases milk production in cattle with little effect on milk composition. Cows eventually increase intake to meet the increased energy demands to support greater milk yield. In lactating cows and heifers, there is evidence that the physiological basis of the response to long days may be an increase in circulating IGF-I. Further, the effect on IGF-I is independent of GH. Feeding of melatonin to mimic short days in heifers produces endocrine responses consistent with the effect of short days on mammary and lean tissue growth. However, feeding melatonin has no effect on lactation and would not be useful as a method to mimic short days in extended light conditions.

With regard to other common management practices, long-day photoperiod can be combined with bST for an additive effect on milk yield. Because bST and 3× milking have additive effects on milk yield, the largest production responses may be realized with the triple combination of bST, long days, and 3× milking, although such a study has not been reported. During the dry period, short-day photoperiodic treatment is appropriate to enhance production of milk in the subsequent lactation. This phenomenon may be of particular interest to producers who find photoperiod manipulation impractical during lactation, such as those that use 3× milking.

We have now developed a framework whereby photoperiod management can be used throughout the life cycle of the dairy cow. During development, long days cause more rapid gain and greater mammary parenchymal growth relative to short-day photoperiods. In the final 2 mo of gestation in heifers and the dry period of multiparous cows, short-day photoperiods are recommended to enhance responsiveness to photoperiod in the subsequent lactation. Long days are recommended during lactation to improve milk yields. Collectively, the efficiency of production in the dairy animal can be dramatically enhanced through photoperiod manipulation and, thus, provide another management tool for

dairy producers to enhance productivity and profitability.

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