

Management of photoperiod in the dairy herd for improved production and health

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ABSTRACT: Environmental influences on lactation efficiency are frequently associated with reductions in milk output. Heat stress, for example, leads to depressed feed intake and, subsequently, losses in production. Conversely, cold stress may limit nutrients available for milk synthesis. Fortunately, one environmental factor, photoperiod, can exert a positive effect on dairy performance when managed properly. Long days have consistently been shown to improve milk yield during established lactation. In addition, photoperiod management can be used to improve heifer growth and maximize accretion of lean tissue, including mammary parenchyma. There is, however, evidence of refractoriness to long day stimulation. Recent work has focused on the dry period as a time when photoperiod manipulation can influence subsequent milk production. In contrast to lactating cows, multiparous cows benefit from

exposure to short days when the dry period is followed by long days or natural photoperiod after calving. Similarly, primiparous animals also respond positively to short days late in pregnancy when subsequently exposed to long days during lactation. Furthermore, emerging evidence suggests that short days positively influence immune function in cattle. Mechanistically, it appears that prolactin has a causal relationship with the observed dairy performance effects during the dry period and on immune function, via altered sensitivity to prolactin through differential expression of prolactin receptor in multiple tissues. The objectives of this paper include a review of fundamental aspects of photoperiod physiology, integration of applied and basic research findings, and development of management recommendations for the entire life cycle of the dairy cow to optimize performance.

Key Words: Photoperiod, Management, Immune Function

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Introduction

The response to photoperiod or the relative duration of light and dark exposure within a day is the most commonly adapted environmental cue used by animals to predict changes in and alter physiological responses to shifts in their physical environment (Gwinner, 1986). Most often the physiological consequence associated with photoperiod is the influence on seasonal reproductive status, although other processes affected by photoperiod include body growth, composition, and pelage changes. Most seasonal impacts on reproductive competence have been selected against in breeding the modern dairy cow, although heat stress remains a major negative influence. Yet seasonal effects on lactation persist and likely result in large measure from the influence of photoperiod (reviewed in Dahl et al., 2000). Al-

though photoperiodic effects on lactation have been studied most frequently in dairy cows, similar responses are observed in other domestic species, including sheep (Bocquier et al., 1990), goats (Terqui et al., 1984), and pigs (Stevenson et al., 1983). Emerging evidence suggests that photoperiod also controls seasonal shifts in immune function and thus animal health (Dowell, 2001).

The first objective of this review is to consider the physiological basis of photoperiodic effects on lactation and immune function and integrate those data to propose a model of how day length alters the response of mammary epithelial cells and leukocytes to result in photoperiodic responses in cell function and metabolism. In addition, recommendations for the application of photoperiod treatment at the production level will be made with emphasis on the dry and lactating state in the mature cow.

Lactating Cows

As summarized in Figure 1, relative to a natural or short day photoperiod (**SDPP**), exposure of lactating

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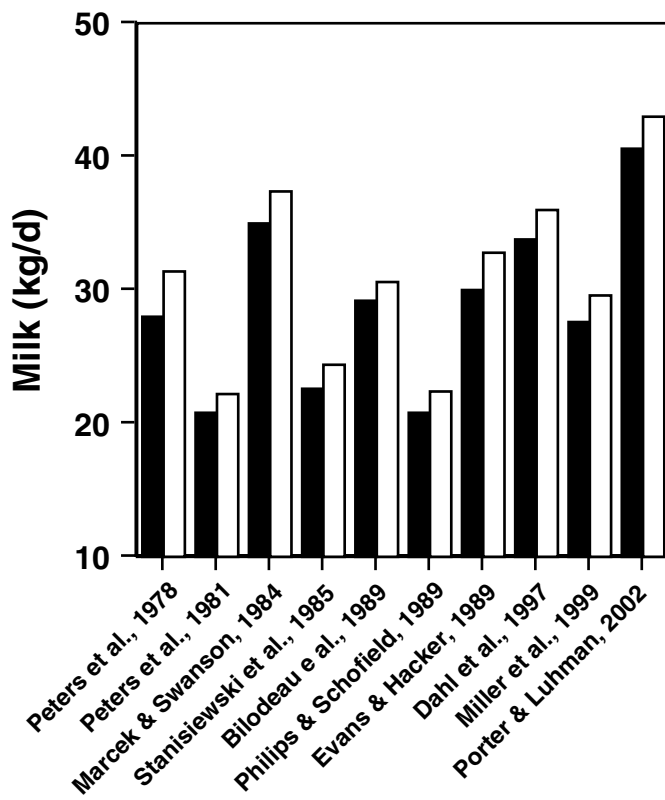


Figure 1. Summary of 10 published studies examining the effect of increased photoperiod on milk yield in lactating cows. Full citations appear in the references section. Solid bars indicate the average daily milk yield (kg/d) of cows on natural photoperiod (range of 8 to 13.5 hr light/d; control), whereas open bars indicate milk yield (kg/d) of cows exposed to extended photoperiod of 16 to 18 hr of light/d.

cows to long days is consistently linked to increases in milk production (referenced in Figure 2). Indeed, Reksen et al. (1999) analyzed records from 1538 herds in Norway and observed that across a spectrum of light exposure from 11.7 to 21.5 h duration, cows with more light produced more milk. However, continuous lighting is not associated with greater milk yield, and, in fact, production between cows on natural photoperiod and those under 24 h of light did not differ (Marcek and Swanson, 1984). This is not surprising as photoperiodic responses occur within a range of entrainment, and continuous lighting is likely outside this range. Milk composition in cows is generally unaffected by photoperiod, although slight depressions of milk fat percentage have been observed (reviewed in Dahl et al., 2000).

Cows respond to long days at any stage of lactation and across a range of production levels. Regression analysis of published data from lactating cows reveals that the response exhibits a slight positive relationship with production level (Figure 2). The response to long days develops gradually but is typically significant after 3 to 4 wk of exposure. The range of duration of long-day exposure in published studies is 8 to 43 wk. Whether

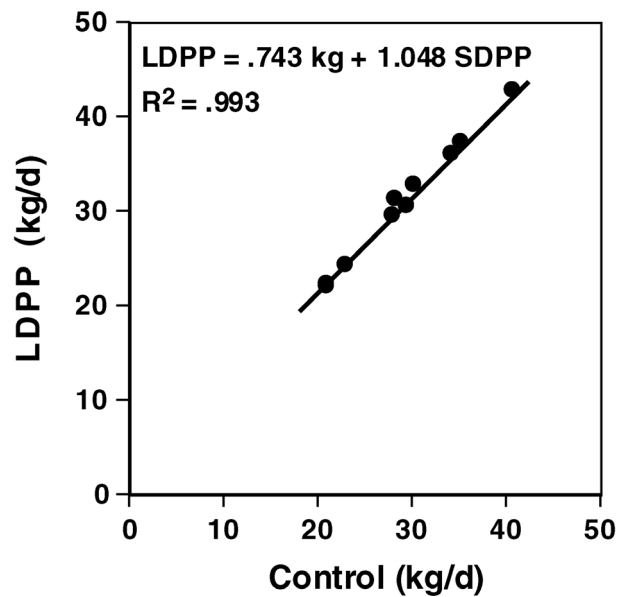


Figure 2. Scatter plot of the response of milk yield to long day photoperiod (LDPP; kg/d) compared with natural photoperiod (control; kg/d) that have been reported in the literature (Peters et al., 1978; Peters et al., 1981; Marcek and Swanson, 1984; Stanisiewski et al., 1985; Bilodeau et al., 1989; Phillips and Schofield, 1989; Evans and Hacker, 1989; Dahl et al., 1997; Miller et al., 1999; and Porter and Luhman, 2002). Regression analysis yields the equation for predicting milk response to long days.

or not cows become refractory to long days from the standpoint of milk yield is unknown, though there is evidence that a break in exposure to long days during the dry period can enhance subsequent production (see below). We have treated cows with long days for up to 20 wk without loss of production increment relative to natural photoperiod, which suggests that treatment responses can persist through an entire lactation, although this has not been confirmed experimentally.

It is now generally accepted that long day responses are mediated via endocrine changes that accompany changes in light exposure. The initial step in the endocrine cascade in response to variable light duration is in the circadian pattern of melatonin secretion. Melatonin release from the pineal is inhibited by light; thus, under natural conditions circulating concentrations are high at night and undetectable during the day (Hedlund et al., 1977). Melatonin secretory patterns are responsive to illumination provided from external sources as well. The relative concentration of melatonin at critical times in the endogenous circadian rhythm then influences physiological interpretation of day length and modulates secretion of other hormones to express shifts in lactation, growth, and health.

Across ages and gender, the most consistent secondary endocrine response to photoperiod is a direct relationship between photophase duration and circulating prolactin (**PRL**; reviewed in Dahl et al., 2000). That is,

long-day exposure increases PRL relative to shorter photoperiods. Evidence argues against a direct role for PRL in the response of lactating cows to long days, as exogenous PRL does not increase (Plaut et al., 1987), and bromocriptine does not depress (Schams et al., 1972) milk yield in lactating cows. Furthermore, long-day responses are observed at cold temperatures, which suppress the PRL response (Peters et al., 1981). Long days are associated with an increase in circulating IGF-I, an increase that is independent of changes in growth hormone (GH) secretion (Dahl et al., 1997; Spicer et al., 1994). The increase in IGF-I observed under long days is also independent of any shift in hepatic response to GH, as expression of GH-receptor 1A is unaffected by photoperiod (Kendall et al., 2003). Yet, the potential galactopoietic action of IGF-I is the subject of some controversy, as milk yield responses to mammary infusion of IGF-I have been inconsistent (reviewed in Tucker, 2000). Recent work in rodents and goats suggests that an interaction between PRL and the IGF system may play a role in lactational persistency, and this is a possible mechanistic explanation for the galactopoietic impact of long days (Flint et al., 2001). Specifically, PRL is inversely related to expression of IGF-binding protein-5 (IGFBP-5), which is considered an apoptotic factor in the mammary gland. The elevated PRL observed under long days would thus be expected to hold IGFBP-5 expression in check and reduce cell loss in the mammary gland. Such an outcome would be consistent with higher persistency and greater overall milk yield. Whereas circulating IGFBP-2 and -3 do not appear to be altered by photoperiod in lactating cows (Dahl et al., 1997), recent evidence using a more sensitive approach to detect IGFBP in steers indicates that IGFBP-3 is elevated under long days relative to short days (Kendall and Dahl, unpublished). If those findings are confirmed in lactating cows, reduced IGF-I clearance may provide a mechanistic explanation for the increases observed under long days. There are no reports that have examined IGFBP-5 directly in cows exposed to different photoperiods.

Dry Cows—Milk Yield Response

In contrast to the lack of effect of exogenous PRL during an established lactation in cattle (Plaut et al., 1987), a robust periparturient PRL surge is essential to complete lactogenesis at calving (Akers et al., 1981). Newbold et al. (1991) observed that long days during the final trimester increased the magnitude of the periparturient PRL surge in heifers. Based on those results, it was hypothesized that an enhanced PRL surge would increase production in the next lactation. Three experiments were completed to test that hypothesis in our laboratories. In the first, 34 multiparous cows were exposed to either 8L:16D or 16L:8D during the dry period to determine the effects on subsequent milk yield (Miller et al., 2000). At calving, all cows returned to the ambient photoperiodic conditions of the herd. As in

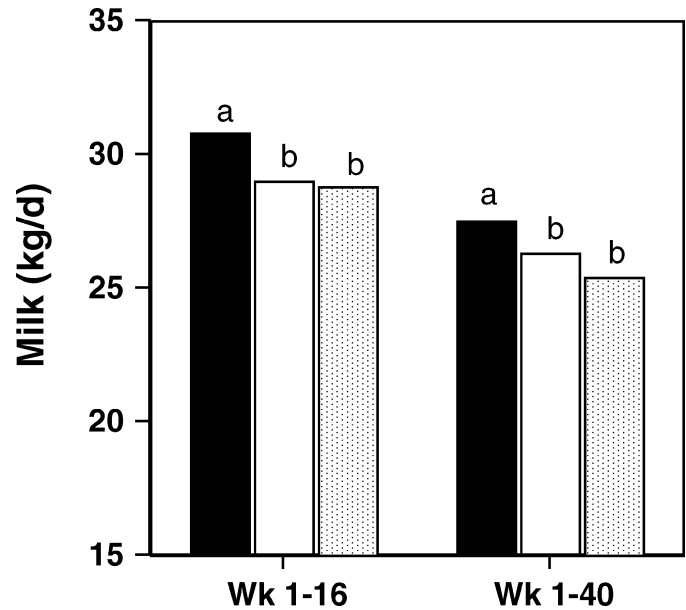


Figure 3. Milk yield response of cows exposed to short days (8L:16D, solid bars), long days (16L:8D, open bars), or long days and fed melatonin (25 mg/d, stippled bars) during the dry period. Bars represent average daily production for wk 1–16 and wk 1–40 of the lactation immediately following treatment. Letters indicate significant differences between treatments (wk 1 to 16, $P < 0.03$; wk 1 to 40, $P < 0.07$). All cows were exposed to long days following parturition. Data adapted from Petitclerc et al., 1998.

Newbold et al. (1991), long days during the dry period caused a larger periparturient PRL surge relative to SDPP. Surprisingly, however, cows exposed to short days during the dry period produced an average of 3.1 kg/d more milk than cows on long days. In the second study, cows were exposed to SDPP or long-day photoperiod (LDPP) during the dry period and then exposed to LDPP after calving (Petitclerc et al., 1998). Again, animals on SDPP during the dry period and transferred to LDPP at parturition produced significantly more milk relative to those exposed to LDPP while dry and after calving (Figure 3). In a third study, pregnant heifers were placed on LDPP or SDPP for the final 60 d before calving (Petitclerc et al., 1990). Similar to the multiparous cows, exposure to LDPP increased concentrations of PRL, but SDPP cows produced more milk in the first lactation. Clearly, a transfer from a shorter photoperiod when dry to a longer photoperiod when lactating maximizes milk yield, but what is the physiological basis for that response?

Cows on SDPP had lower circulating PRL at calving relative to the LDPP cows (7.7 vs. 15.2 ng/ml). Considered with the PRL results, these data suggest that increasing the PRL surge via LDPP is without effect on subsequent yield of milk, but other factors associated with SDPP were stimulatory. However, a third group of cows in the second study treated with long days and

fed melatonin (25 mg/d) in the middle of the photophase to mimic a short day pattern did not yield more milk relative to the LDPP group (Figure 3), despite a reduction in circulating PRL relative to the LDPP cows (9.7 vs. 15.2 ng/ml). Yet previous use of melatonin feeding to mimic a SDPP in lactating cows has not been successful in altering the milk yield response; thus, melatonin replacement may not be an appropriate model for a short day in mature cows with regard to milk production (Dahl et al., 2000).

The observed effect of SDPP during the dry period (and late pregnancy in primiparous animals) may be due to the fact that animals become refractory to a constant light pattern and exposure to SDPP resets a cow's responsiveness to the stimulatory signal. An alternative interpretation of the data from the three studies presented above is that LDPP during the dry period suppressed milk yield in the subsequent lactation. Such an interpretation would be consistent with previous studies in sheep and quail that examined the influence of direction of photoperiodic change (i.e., exposure to increasing vs. decreasing photoperiod) on responses of the reproductive systems (Robinson and Follett, 1982; Robinson and Karsch, 1987). However, comparison of 305-d mature equivalent data between the lactation preceding the LDPP treatment and the lactation following (i.e., the full record of the data reported in Miller et al., 2000) revealed no difference between years. This suggests that the LDPP treatment during the dry period was not detrimental to the subsequent lactation. Rather, SDPP during the dry period stimulated subsequent production.

Further confirmation of the importance of dry period light exposure on subsequent milk yield has emerged from examination of seasonal effects of parturition on milk production. It has long been known that cows that calve in July and August in the Northern Hemisphere, when day length and temperature are near maximum, produce less milk than contemporaries that calve in November and December (Wunder and McGilliard, 1971; Barash et al., 1996). This influence of season of calving on milk yield has traditionally been attributed to heat induced depression of intake and subsequent milk production (Wunder and McGilliard, 1971; Wolfenson et al., 1988). However, recent work suggests that a majority of the seasonal effect can be accounted for by environmental factors during the dry period, specifically photoperiod. Aharoni et al. (2000) examined the records of more than 2000 cows and found that photoperiod exposure during the final 21 d of the dry period was inversely related to milk yield in the subsequent lactation. That is, exposure to SDPP meant that cows produced 2.1 kg more milk per day than exposure to a LDPP. Extrapolated out for an entire lactation, this would be an increase of 640 kg. Putting that into perspective, that would be about 67% of the expected increase in response to bST treatment according to label instructions (Bauman, 1999).

PRL Sensitivity in Peripartum Cows

The apparent paradox of photoperiodic effects on lactating vs. dry cows may be due to the different impacts of PRL and IGF-I during each physiological state. Specifically, we believe that PRL is exerting a developmental effect in the dry/transition period, and this response is not present once lactation is fully established. In contrast, the impact of elevated IGF-I during lactation is a metabolic action at the mammary gland, which would be absent in the nonlactating state. With regard to PRL, our theory is that elevated PRL during the dry period produces a "PRL resistance" at the mammary gland. At the time of parturition, the periparturient PRL surge is critical to the secondary stage of lactogenesis (Akers et al., 1981), and early in lactation the interplay of PRL and PRL-receptor (**PRL-r**) may be important to maximize mammary epithelial cell recruitment and differentiation. Cows on a SDPP during the dry period and transferred to a longer photoperiod in early lactation would therefore be expected to have greater PRL-r expression and an increasing concentration of circulating PRL. Cows on long days in the dry period would have reduced PRL-r expression and a depressed PRL secretory stimulus due to negative feedback. Therefore, an increase in circulating PRL in the periparturient stage layered over a greater number of PRL-r should maximize cell numbers and hence lactation. Direction of change in photoperiod is therefore as important as absolute duration with regard to the dry cow response (Robinson and Follett, 1982; Robinson and Karsch, 1987).

A number of observations support this hypothesis regarding PRL resistance. Indeed, chronic elevation of PRL suppresses PRL-r expression (Barash et al., 1983; Kazmer et al., 1986; Smith et al., 1989). Other physiological perturbations that elevate PRL, such as high temperature, also have a negative impact on milk yield in the next lactation (Barash et al., 1996). In contrast to the previously mentioned lack of effect of PRL on milk yield in cows once lactation is established, several reports suggest that PRL elevations may be important early postpartum. These include the stimulatory effect of PRL immediately postmilking in goats (Jacquemet and Prigge, 1991) and the stimulatory effect of multiple daily milking (e.g., 6 times a day) early in lactation on milk yield for the remainder of the lactation (Bar-Peled et al., 1995; Henshaw et al., 2000). The same multiple daily milking scheme did not induce permanent effects when imposed on midlactation cows (Bar-Peled et al., 1995). We have recently observed that frequent milking in early lactation (i.e., four vs. two milkings per day) induces a significant, though transient, increase in PRL-r mRNA using lymphocytes as a proxy for mammary cells (Dahl et al., 2002). Though circumstantial, these observations all support the concept that increasing PRL with a higher relative PRL-r expression produces maximal, permanent increases in milk secretory capacity for that lactation when imposed during the

immediate postpartum period. But what is the effect of photoperiod or PRL itself on PRL-r expression in cattle? We have used PRL-r mRNA as an index of PRL-r expression in liver, lymphocytes, and mammary parenchyma in steer calves (Auchtung et al., 2002a). Expression of PRL-r mRNA was inversely related to plasma PRL concentrations; thus, SDPP increased PRL-r mRNA relative to LDPP. More importantly, when the same calves had photoperiodic treatments reversed, the effects on PRL and PRL-r reversed also, suggesting that photoperiodic shifts in PRL secretion mediated these shifts in PRL-r expression. In addition, relative expression of PRL-r moved in parallel in the three tissues, indicating that lymphocytes can be used to track shifts in PRL-r expression in other tissues without the invasive disruption of a biopsy.

Photoperiod and Mammarygenesis

In addition to the impact in the mature cow, photoperiod manipulation has effects on mammary development. Relative to short days, parenchymal cell number was greater in heifers exposed to long days during the prepubertal period (Petitclerc et al., 1985). Because long days hasten puberty (reviewed by Hansen, 1985), a portion of that growth may be associated with the acceleration in gonadal steroid secretion associated with long day treatment. However, long days also increase parenchymal cell number after puberty, suggesting that other factors in addition to gonadal steroids play a role (Petitclerc et al., 1985). Certainly the effects of photoperiod on PRL and IGF-I would be consistent with greater mammary growth, though definitive experiments have not been reported.

Photoperiodic Effects on Health

In the wild, animals must adjust their growth, reproduction, and lactational priorities to meet the energetic demands and resource limitations that occur on a seasonal basis, so to they are likely to face seasonal shifts in pathogens. Thus, annual patterns of variation in immune function have been observed in many species, yet the physiological foundation for those patterns is unknown (Dowell, 2001). Because of the linkage to other seasonal responses, a role for photoperiod has been investigated. In hamsters, photoperiod alters immune function (Yellon et al., 1999), with short days reducing the severity of infectious responses (Bilbo et al., 2002a, 2002b). Photoperiod induced shifts in cortisol and PRL have been implicated in the development of this altered immune function in rodents, and preliminary evidence from one of our laboratories suggests that PRL serves a similar role in the bovine.

Because PRL is considered a cytokine and PRL-r is a member of the cytokine receptor superfamily (Kelly et al., 1991), our initial inquiry related to identification of PRL-r on lymphocytes. In steer calves, quantification of PRL-r mRNA using real-time PCR led to the observa-

tions that bovine lymphocytes express short and long forms of PRL-r (Auchtung et al., 2001, 2002b), and expression of both forms of PRL-r increases under SDPP, inverse to the shift in PRL secretion observed with that photoperiod (Auchtung et al., 2001). Further, SDPP was associated with greater lymphocyte proliferation *in vitro*, and this was reversed with reversal of photoperiod treatment (Auchtung et al., 2002a). These observations support the hypothesis that short days enhance immune function in calves, yet questions remain regarding application to mature cows.

The transition period from the dry to lactating state is the acme of immunosuppression in the lactation cycle. Because cows exposed to SDPP when dry produce more milk in the next lactation, it became critical to evaluate the effect of SDPP on immune function to ensure that further immunosuppression did not occur and negate the production effect. Preliminary results suggest that cows on SDPP when dry had greater PRL-r expression and lower circulating PRL relative to LDPP cows. In addition, SDPP dry cows had increased lymphocyte proliferation and chemotaxis response to interleukin-8 (Auchtung and Dahl, unpublished). Cows on SDPP also subsequently produced more milk. These results suggest that exposure to SDPP during the dry period not only improve production in the subsequent lactation but also potentially improve animal health and well-being.

With regard to health, it is important to consider the potential influence then of LDPP in lactating cows. That is, will cows exposed to LDPP to increase production have higher incidence of disease? The photoperiod literature does not support this speculation, as there were no reports of increased mastitis or other infectious disease in cows on LDPP relative to natural photoperiod. It is most likely that LDPP exposure would not heighten the incidence of disease, as the risk is greatest during the transition phase, and once lactation is fully established, disease incidence is dramatically reduced. In addition, the increment from a natural photoperiod to LDPP may be insufficient to significantly influence immune function. These questions remain, however, as areas requiring further investigation.

Summary and Recommendations

Some 25 yr after the initial report of galactopoietic effects of long days in cattle, new findings continue to increase our understanding of the role of photoperiod in production and health. Considering the research to date, we can make the following recommendations regarding light exposure during the life cycle of the cow. First, heifers should be exposed to LDPP during the postweaning phase until puberty to maximize mammary parenchymal growth. Data for yearling heifers is lacking at present. However, during the final 60 d of pregnancy, primiparous heifers and dry cows should be under SDPP to maximize production in the next lactation and enhance immune function in the transition period. During lactation, exposure to LDPP is rec-

ommended to increase milk yield, particularly in cases where dry period exposure to SDPP is not possible.

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