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Heat stress in lactating dairy cows: a review

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Abstract

Our objective was to provide a review of factors influencing heat stress in lactating dairy cows and how it affects milk production. In warmer parts of the world, during summer months in the United States, and in other temperate regions, reduced milk production resulting from heat stress counteracts tremendous genetic progress achieved in increasing milk production. Genetic progress in milk production is closely related to increased feed intake. High feed intake results in raised metabolic heat increment. High metabolic heat increment requires effective thermoregulatory mechanisms to maintain body temperature in a thermoneutral zone and in physiological homeostasis. Cows can succumb to hyperthermia if they fail to maintain thermoneutrality. Accurate measurement of when cows enter heat stress is complicated because the responses to heat stress affect not only the energy balance, but also water, sodium, potassium and chlorine metabolism. Water, sodium, potassium and chlorine are important constituents of sweat, and sweating is a major, if not the most important, thermoregulatory mechanism used to dissipate excess body heat. Due to high metabolic heat increment, and especially in the warmer months, high-producing dairy cows may enter heat stress much earlier than their lower-producing counterparts and than currently thought, or extra heat has been accommodated by physiological adaptations. Should this be the case, then strategies to reduce heat stress must be developed to enable cows to express their full genetic potential. The thermoneutral zone, heat production and heat gain, heat dissipation mechanisms, and how the lactating cow responds to heat stress are discussed.

Keywords: Heat stress; Responses; Lactating cows; Dairy cattle

1. Introduction and justification

The thermal environment is a major factor that can negatively affect milk production of dairy cows, especially in animals of high genetic merit. Dairy cattle research has tended to concentrate on genetic improvements to increase milk production and on nutrient supply to the cow during early lactation. Little attention has been paid to the thermoregulatory ability of the modern cow as her capacity to produce milk has increased.

The question arises whether the temperature at which cows currently start experiencing heat stress has shifted to a lower point, considering that in-

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creased milk production is positively correlated to both feed intake and metabolic heat production. The metabolism of an animal is always in a state of dynamic equilibrium in which the influx of nutrients is balanced by the production of energy in catabolic and anabolic processes. Cows require nutrients for, among other things, maintenance of biological processes, reproduction, and lactation. The separation of metabolism into maintenance and production is somewhat artificial because energy metabolism is affected by complex interrelationships among all physiological processes. Early research to measure heat and moisture production/loss from animals had been based on the standard metabolic rate (SMR) (Gordon et al., 1968), or basal metabolic rate (BMR) (Hayssen and Lacy, 1985). (Abbreviations used in this paper are listed in Table 1.) The concept of BMR (or fasting heat production) originates from the works of Kleiber (1932) and Brody (1945) which related it to the metabolic body size (body weight (BW) in the form of a power function in an interspecies comparison of mature animals). The concept of metabolic body size has been used as a basis for scaling other physiological/metabolic parameters, such as food intake and drug metabolism, thereby removing the effects of body size. To attain SMR or BMR, an animal must be post-absorptive, awake, at rest, and in a thermo-neutral environment (Gordon et al., 1968); however, cows under commercial production conditions do not meet these constraints. Heat production at BMR has already been reviewed (Brody, 1945; Hayssen and Lacy, 1985) and will not be discussed further.

Nutrient intake by high-producing cows is closely related to the amount of milk produced. The process of metabolizing nutrients generates heat, which contributes to maintaining body temperature in a cold environment. In a warm climate this heat has to be dissipated if thermal neutrality, a prerequisite for normal physiological function, is to be maintained. This complex interplay of physical and environmental effects influences the physiological functions of the cow and affects not only milk production but also the efficiency and profitability of dairy enterprises. We estimated the amount of heat stress encountered by dairy cows in the United States using records from the National Climatic Data Center (part of the Department of Commerce, National Oceanic and Atmospheric Administration) for the mean number of days per year with maximum temperatures of 32.2 °C or higher and the mean number of cooling degree-days (base 18.3 °C) per year for weather stations across the country. Cooling degree-days are used to estimate the amount of energy required to

Table 1
Abbreviations

Symbol	Description
ARC	Agricultural Research Council
BMR	Basal metabolic rate
BW	Body weight
DCAB	Dietary cation–anion balance
DM	Dry matter
DMI	Dry matter intake
FCM	Fat corrected milk
FI	Feed intake
GE	Gross energy
H_f	Heat of fermentation
Hg	Mercury
HI	Heat increment
HP	Heat production
HR	Heart rate
ICBA	Israel Cattle Breeders Association
J	Joule
$kg^{0.75}$	Metabolic body size
kJ	Kilojoule
k_l	Efficiency of energy utilization for milk production
k_m	Efficiency of energy utilization for maintenance
LCT	Lower critical temperature
ME	Metabolizable energy
meq	Milliequivalents
NE	Net energy
NE_l	Net energy lactation
NE_m	Net energy maintenance
NRC	National Research Council
p_{CO_2}	Partial pressure of carbon dioxide
p_{O_2}	Partial pressure of oxygen
PROD	Production
RH	Relative humidity
SMR	Standard metabolic rate
SODIN	Sodium intake
T_3	Triiodothyronine
T_4	Thyroxine
T_d	Average dry bulb temperature
THI	Temperature–humidity index
TMIN	Weekly minimum temperature (°C)
TNZ	Thermoneutral zone
T_r	Rectal temperature
UCT	Upper critical temperature
USDA	United States Department of Agriculture
VFA	Volatile fatty acids
WI	Water intake

maintain comfortable indoor temperatures and are computed from each day's mean temperature [(minimum + maximum)/2] by accumulating the difference between the mean temperature and 18.3 °C for days that it exceeded this temperature. A weighted average for these variables was then calculated for the 100 counties in United States with the most dairy cows in 1997. The top 100 counties had from 19,368 to 277,922 cows and accounted for 4.3 million (48%) of the 9.1 million dairy cows in the country. The average dairy cow experienced 47 days when the maximum temperature was 32.2 °C or higher and 625 cooling degree (Celsius)-days per year. Temperature data alone do not tell the whole story; however, similar information for the heat index in the US is not available.

For the ~110,000 dairy cows in Israel, heat stress was quantified in a similar manner. Temperature and relative humidity data, based on a temperature humidity index (Kibler, 1964), for 17 locations were used (Gat et al., 1999). Heat units, positive differences between the index and 22 units, were accumulated daily from May through October. Total heat units for each location were then combined with milk production data (Israel Cattle Breeders Association, 1997) for the corresponding districts in 1996 to calculate a weighted average. The average cow in Israel was exposed to 196 heat units during the 6-month period.

We hypothesized that the thermal regulatory physiology of the cow may have changed in response to genetic selection for increased milk production. This hypothesis is justified by the fact that data from the USDA reveal a 338% increase in average milk production per cow per 300-day lactation between 1940 and 1995, from 2096 kg (2090 kg of 4% FCM) to 7462 kg (7080 kg 4% of FCM) (Table 2). In Israel the average milk production per year has increased from 3690 kg (3516 kg of 4% FCM) to 10,447 (9293.8 kg of FCM) between 1934 and 1997 (Table 3). The average milk production per cow per 300-day lactation is higher now and is projected to increase further in the future.

The lactating cow uses metabolizable energy (ME) for milk production at an average efficiency (q) of 65% (Moe et al., 1970). It should be mentioned that heat increment (HI) during milk synthesis is also dependent on the quality and quantity of feed that the animal consumes. The quality of dairy cattle feed has changed enormously between 1940 and 1995. Using this information and the fact that the gross energy (GE) content of 4% FCM is 3.14 MJ/kg, we calculated the HI. The classical work on heat stress (Brody, 1945) was done close to when dairy record keeping started in the US (1940) and is used as a point of departure. Against this background, we calculated the average HI between 1940 and 1995, in the US, at four efficiencies of milk production, $q = 50$, 60, 65 and 70% (Table 4; and for 1934 to 1997 in Israel, Table 5), to estimate the impact that changes in efficiency would have on HI. The results indicated that increased milk production is related to elevated HI. Total milk production and HI have increased over time; however, the rate of increase of HI has been slower than of milk production (Fig. 1, US; Fig. 2, Israel).

Table 2
Average milk production per cow per 300-day lactation from 1940 to 1995 in the US

Year	Milk (kg/year)	Milk (kg/day)	4% FCM[a] (kg/year)	4% FCM (kg/day)	Fat (kg/year)	Fat (kg/day)	Fat (%)
1940	2096	7	2090	7	83.5	0.28	3.97
1950	2410	8	2393	8	95.3	0.32	3.96
1960	3188	10.6	3072	10.2	119.8	0.4	3.76
1970	4423	14.7	4198	14	161.9	0.54	3.66
1975	4699	15.7	4472	14	172.8	0.58	3.68
1980	5394	18	5117	17.1	197.3	0.66	3.65
1985	5908	19.7	5615	18.7	216.8	0.72	3.67
1990	6705	23.4	6349	21.2	244.5	0.81	3.65
1995	7462	24.9	7080	23.6	273.1	0.91	3.66

[a] 4% fat-corrected-milk or FCM is milk corrected to 4% fat, and is expressed in the formula $\mathrm{FCM} = 0.4M + 15F$, where M is the weight of milk and F is the weight of fat, with milk and fat all being in the same units.

Table 3
Average annual milk production per Holstein cow from 1934 to 1997 in Israel

Year	Milk (kg/year)	Milk (kg/day)	4% FCM[a] (kg/year)	4% FCM (kg/day)	Fat (kg/year)	Fat (kg/day)
1934	3690	10.1	3516	9.6	136	0.37
1944	4227	11.6	3940.8	10.8	150	0.41
1954	4197	11.5	3913.8	10.7	149	0.41
1964	5694	15.6	5067.6	13.9	186	0.51
1974	6833	18.7	6033.2	16.5	220	0.60
1984	8734	23.9	7798.6	21.4	287	0.79
1994	9748	26.7	8429.2	23.1	302	0.83
1997	10 447	28.6	9293.8	25.5	341	0.93

[a] 4% fat-corrected-milk or FCM is milk corrected to 4% fat, and is expressed in the formula FCM $= 0.4M + 15F$, where M is the weight of milk and F is the weight of fat, with milk and fat all being in the same units.

Table 4
Average daily heat increment of dairy cows from 1940 to 1995 at four efficiencies of milk production in the US; (a) $q = 50\%$; (b) $q = 60\%$; (c) $q = 65\%$; (d) $q = 70\%$

Year	4% FCM[a] (kg/year)	MJ HI/day[b] ($q = 50\%$)	MJ HI/day ($q = 60\%$)	MJ HI/day ($q = 65\%$)	MJ HI/day ($q = 70\%$)
1940	2090	21.9	14.6	11.8	9.4
1950	2393	25	16.7	13.5	10.7
1960	3072	32.1	21.4	17.3	13.8
1970	4198	43.9	29.3	23.7	18.8
1975	4472	46.8	31.2	25.2	20.1
1980	5117	53.5	35.7	28.8	22.9
1985	5615	58.7	39.2	31.6	25.2
1990	6349	66.4	44.2	35.8	28.5
1995	7080	74.1	49.4	38.9	31.7

[a] 4% fat-corrected-milk or FCM is milk corrected to 4% fat, and is expressed in the formula FCM $= 0.4M + 15F$, where M is the weight of milk and F is the weight of fat, with milk and fat all being in the same units.

[b] MJ HI/day is heat increment in megajoules per day, calculated from milk production data from the National Agricultural Statistics Service, USDA.

Table 5
Average daily heat increment of Holstein cows from 1934 to 1997 at four efficiencies of milk production in Israel; (a) $q = 50\%$; (b) $q = 60\%$; (c) $q = 65\%$; (d) $q = 70\%$

Year	4% FCM[a] (kg/year)	MJ HI/day[b] ($q = 50\%$)	MJ HI/day ($q = 60\%$)	MJ HI/day ($q = 65\%$)	MJ HI/day ($q = 70\%$)
1934	3516	30.2	20.1	16.3	12.9
1944	3940.8	33.9	22.6	18.3	14.5
1954	3913.8	33.7	22.5	18.1	14.4
1964	5067.6	43.6	29.1	23.5	18.7
1974	6033.2	51.9	34.6	27.9	22.2
1984	7798.6	67.1	44.7	36.1	28.8
1994	8429.2	72.5	48.3	39.0	31.1
1997	9293.8	80.0	53.3	43.1	34.3

[a] 4% fat-corrected-milk or FCM is milk corrected to 4% fat, and is expressed in the formula FCM $= 0.4M + 15F$, where M is the weight of milk and F is the weight of fat, with milk and fat all being in the same units.

[b] MJ HI/day is the heat increment in megajoules per day, calculated from milk production data (Israel Cattle Breeders Association, 1997).

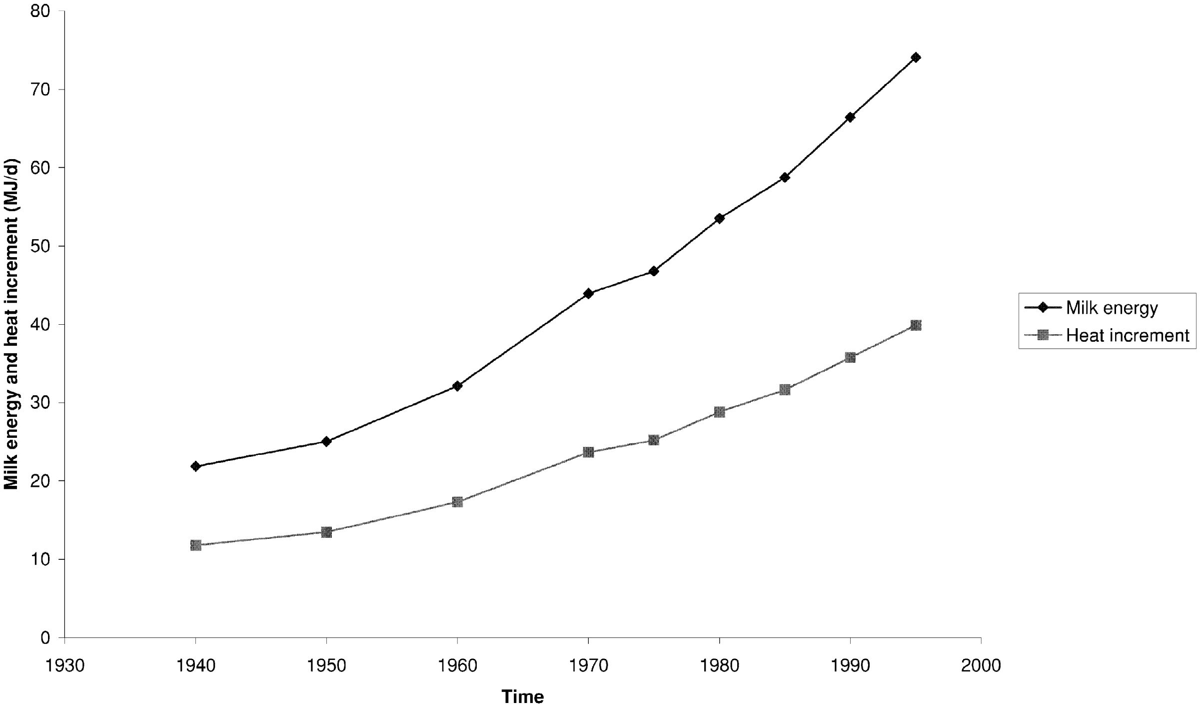

Fig. 1. Milk energy and heat increment of lactating cows in the US from 1940 to 1995 calculated from USDA annual milk production data. Conversion of ME into milk energy at an average efficiency of 65% was assumed.

Furthermore, the average BW of dairy cows has increased over time as cows have been selected to produce more milk (Fig. 3). Data from Ragsdale (1934), Davis and Hathaway (1956) and Heinrichs and Hargrove (1987) suggest that, over time, the size of 24-month-old Holstein heifers has increased by 46 kg (or about 10%) from 485 to 531 kg. Larger cows have larger gastrointestinal tracts that allow them to consume and digest more feed. This in turn provides more substrates for milk synthesis.

There is an apparent lack of realization that changes in the physical and genetic constitution of cows may have affected their thermoregulatory capability as well as how they cope with heat stress. The objective of our review was to focus on responses of high-producing dairy cows to heat stress. The literature on this particular topic is scant and does not provide a holistic view of factors that influence the incidence of heat stress in high-producing dairy cows, especially during early lactation. The thermoneutral zone, heat production and heat gain, heat dissipation mechanisms, as well as how the lactating cow responds to heat stress are reviewed.

2. Heat stress in dairy cows

Yousef (1985) defined stress as the magnitude of forces external to the body which tend to displace its systems from their resting or ground state. In this light, heat stress for the dairy cow can be understood to indicate all high temperature-related forces that induce adjustments occurring from the sub-cellular to the whole animal level to help the cow avoid physiological dysfunction and for it to better fit its environment. The endeavor by homeotherms to stabilize body temperature within fairly narrow limits is essential to control biochemical reactions and physiological processes associated with normal metabolism (Shearer and Beede, 1990). In order to maintain homeothermy, an animal must be in thermal equilibrium with its environment, which in-

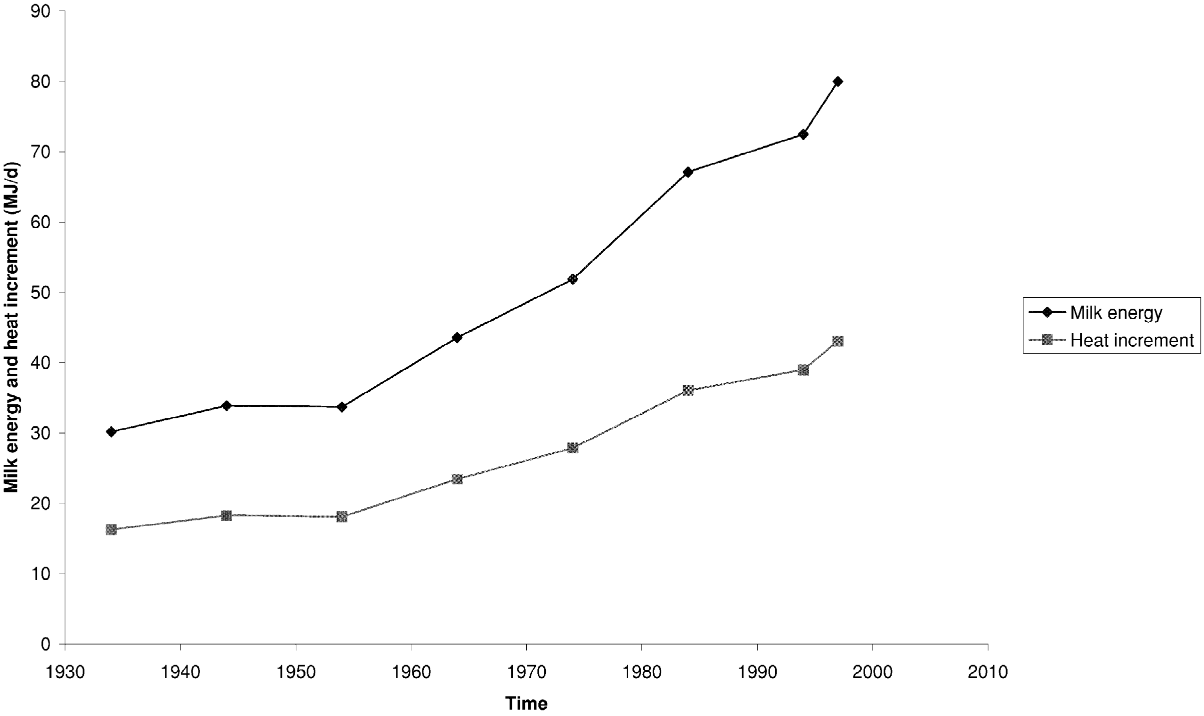

Fig. 2. Milk energy and heat increment of lactating Holstein cows in Israel from 1934 to 1997 calculated from average annual milk production data (Israel Cattle Breeders Association, 1997). Conversion of ME into milk energy at an average efficiency of 65% was assumed.

cludes radiation, air temperature, air movement and humidity.

Lactating dairy cows prefer ambient temperatures of between 5 and 25 °C, the 'thermoneutral' zone (TNZ) (Roenfeldt, 1998). At ambient temperatures above 26 °C, the cow reaches a point where she can no longer cool herself adequately and enters heat stress. Body temperature is usually maintained by thermoregulatory systems within 1 °C of normal under ambient conditions that do not impose severe heat stress (Bligh, 1973). Thermal stress and thermal relief have been assessed by measuring body temperature (Fuquay et al., 1979). Body temperature of dairy cattle shows great susceptibility to hot weather (Akari et al., 1984); therefore, it is a sensitive indicator of thermal stress. McDowell et al. (1976) also suggested that the temperature–humidity index (THI) could be used as an indicator of thermal climatic conditions. The THI is calculated from the wet and dry bulb air temperatures for a particular day according to the following:

$$\mathrm{THI} = 0.72(W + D) + 40.6 \qquad (2.1)$$

where W is wet bulb and D is dry bulb temperature in °C.

Temperature–humidity index values of 70 or less are considered comfortable, 75–78 stressful, and values greater than 78 cause extreme distress with lactating cows being unable to maintain thermoregulatory mechanisms or normal body temperatures. Lemerle and Goddard (1986) reported that, although rectal temperature only increased when THI was greater than 80, the respiration rate would begin to increase above a THI value of about 73 and would probably increase steeply at THI values >80. This finding suggests that homeostatic mechanisms, in-

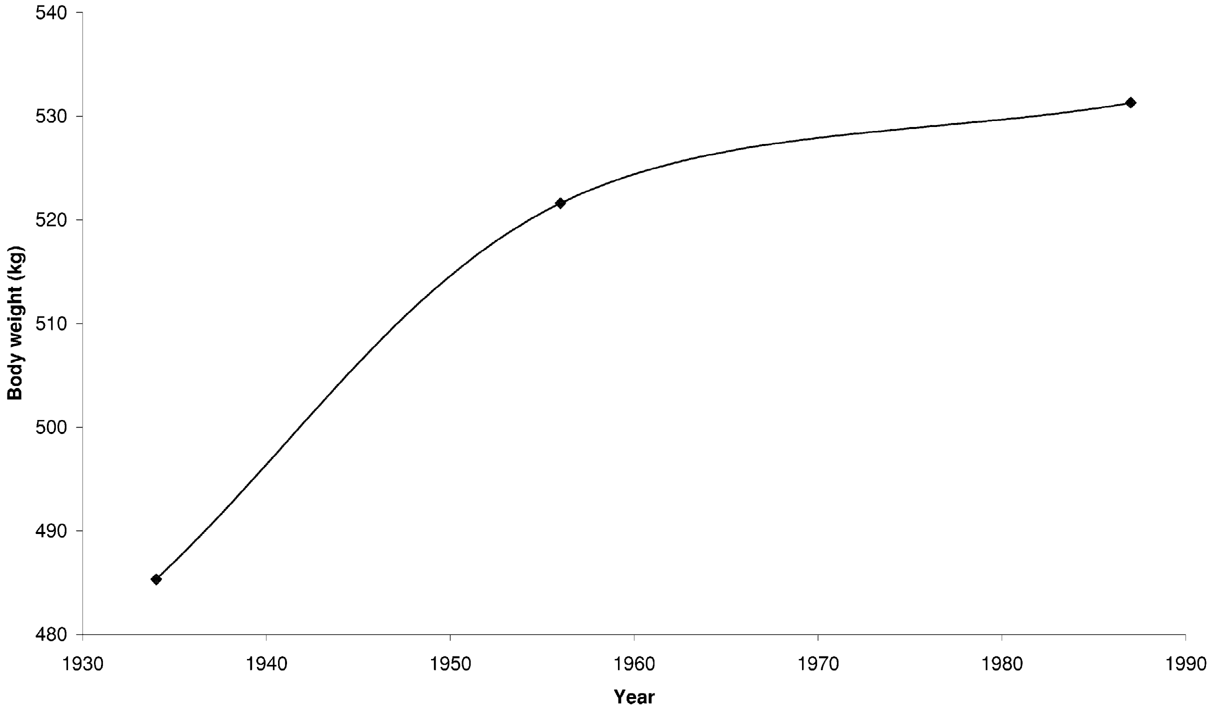

Fig. 3. Bodyweight of Holstein heifers at 24 months of age between 1934 and 1987 in the US (Ragsdale, 1934; Davis and Hathaway, 1956; Heinrichs and Hargrove, 1987).

cluding increased respiration, can prevent a rise in rectal temperature until the THI reaches 80. This is similar to the critical THI level of 78 quoted by McDowell et al. (1976). When environmental temperature exceeds the zone of thermoneutrality, milk composition changes and production declines (Coppock, 1978).

Working with two pairs of Jersey cows exposed to either 15 or 30 °C air temperature, Bandaranayaka and Holmes (1976) found that the fat and protein contents of milk decreased ($P<0.05$) at 30 °C when intake was kept equal at both temperatures. Bandaranayaka and Holmes (1976) also reported that the proportion of shorter-chain fatty acids (C_6–C_{14}) in milk fat decreased ($P<0.05$) at 30 °C. On the other hand, the proportions of long-chain fatty acids increased ($P<0.05$) at 30 °C for $C_{18:0}$ alone, but only tended to increase ($P<0.10$) for the acids $C_{18:0}$, $C_{18:1}$, $C_{18:2}$ and $C_{18:3}$ combined. The decrease in milk fat and protein content was positively correlated to reductions in proportions of acetate in the rumen contents and to a small reduction in ruminal pH at 30 °C. Protein percentage in the milk decreased in all cows during the treatment period, with decreases being greater in cows at 30 °C than in cows at 15 °C ($P<0.01$ a.m.; $P<0.05$ p.m.). Temperature did not affect milk production ($P>0.10$) and the lactose percentage (5.32–5.48%) in milk in these studies. Heat stress is characterized by elevated respiration rates and rectal temperatures, and has been implicated in impaired metabolism (Bandaranayaka and Holmes, 1976), and in poor reproductive performance (Ingraham et al., 1974) in dairy cattle independent of any effects on feed intake. Although specific temperatures were not listed, Coppock et al. (1982) concluded that high-producing cows are affected more than low-producing cows because the zone of thermal neutrality shifts to lower temperatures as milk production, feed intake, and metabolic heat production increase.

3. Thermoneutral zone

The TNZ can be understood as the zone of minimal heat production at normal rectal temperature. Within the TNZ (Fig. 4), minimal physiological costs and maximum productivity are normally achieved (Johnson, 1987). Generally, the TNZ range (from lower critical temperature (LCT) to upper critical temperature (UCT)) depends on age, species, breed, feed intake, diet composition, previous state of temperature acclimation or acclimatization, production, specific housing and pen conditions, tissue insulation (fat, skin), external insulation (coat), and behavior of an animal (Yousef, 1985). Igono et al. (1992) measured the highest milk production in Holstein cows under a desert environment during optimal thermal neutral periods that were characterized by ambient temperatures below 21 °C throughout the day. McArthur and Clark (1988) concluded that the TNZ was related to the heat and water balances of animals. The farther an animal moves away from its preferred body temperature, the more detrimental temperature becomes to productive processes. McDowell et al. (1976) reported that even small upward shifts in core temperature have profound effects on tissue and endocrine function that, in turn, can reduce fertility, growth, lactation, and the ability to work. A stable body temperature in

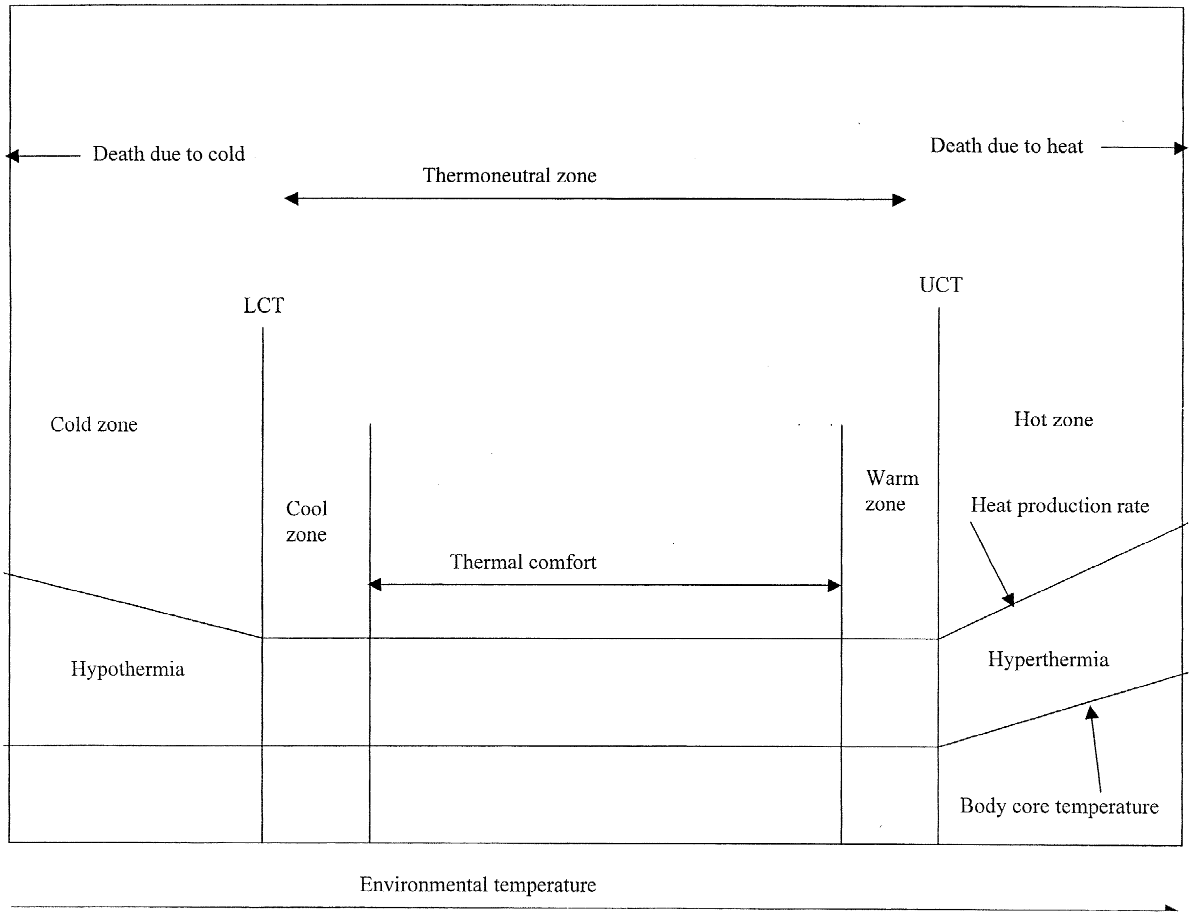

Fig. 4. Schematic relationship of the animal's body core temperature, heat production and environmental temperature (adapted from Curtis, 1981). LCT, lower critical temperature; UCT, upper critical temperature.

the TNZ is a prerequisite for maximal productivity in dairy cattle (Fig. 4).

3.1. Lower critical temperature

The ambient temperature below which the rate of heat production (HP) of a resting homeotherm must increase to maintain thermal balance is the LCT (Fig. 4). This implies that the rate of HP is dependent upon ambient thermal demand below the LCT (Yousef, 1985). At environmental temperatures above the LCT, body temperature is maintained until the UCT (Alexander, 1974). The estimate of LCT for cows producing 30 kg of FCM/day is given as a range from −16 to −37 °C (Hamada, 1971). Non-evaporative heat loss declines as ambient temperatures rise above the LCT making the animals more dependent on peripheral vasodilatation and water evaporation to enhance heat loss and to prevent a rise in body temperature.

3.2. Upper critical temperature

The UCT (Fig. 4) is the air temperature at which the animal increases heat production as a consequence of a rise in body temperature resulting from inadequate evaporative heat loss (Yousef, 1985). Estimates of UCT have been obtained from studies in which dairy cows were exposed for short periods to constant temperatures in climatic chambers (Kibler, 1964). When the thermal load exceeds the evaporative heat loss capacity, body temperature rises and, if unchecked, the animal dies from hyperthermia. In hot climates, the potential for non-evaporative heat loss is reduced and animals rely on the evaporation of water to dissipate any excess heat generated by metabolism (McArthur and Clark, 1988).

The UCT is given as 25–26 °C for dairy cows, irrespective of previous acclimatization or of their milk production (Berman et al., 1985). The estimation of the UCT and its specification as 25–26 °C, irrespective of previous acclimatization or of milk production, contradicts the conclusion of Yousef (1985) that the TNZ varies with physiological state and other environmental conditions. At or below the UCT and above the LCT, Holstein cattle may maintain a stable body temperature. Above the UCT, an increase in body temperature negatively influences performance, reducing milk production and changing milk composition, and the cow enters heat stress.

The UCT can be inferred from thermoregulatory functions like increased sweating and respiratory water loss, and increased body temperature (Berman et al., 1985). Evaporative water loss from the skin increases at air temperatures above 20 °C (Berman, 1968). Igono and Johnson (1990) found high-producing cows in early lactation to be more sensitive to heat stress, and milk production declined significantly when rectal temperatures exceeded 39 °C for more than 16 h. In addition, Purwanto et al. (1990) found cows at high (31.6 kg/day) and medium (18.5 kg/day) milk productions generated 48.5 and 27.3% more heat, respectively, than dry cows. This, they attributed to high milk production coupled with large nutrient intake and concomitant greater heat production.

Maltz et al. (1984), working with goats, as well as Frisch and Vercoe (1977) working with cattle, suggested that breeds of ruminants which are well adapted to desert environments have a greater capability than non-desert breeds to counter the stressful effects induced by high heat loads.

3.3. Adaptations

The ability to regulate temperature is an evolutionary adaptation that allows homeotherms to function in spite of variation in ambient temperature (Bitman et al., 1984); this ability also allows temperature to be used as a signal to control physiological processes. The fact that the highest milk productions have been achieved in temperate climates and that high genetic potential cows transferred to tropical environments have failed to realize their theoretical production capacity underscores the interaction of the animal and the environment.

Mullick (1960) found buffalo to be better adapted to hot tropics than cattle because of their heat tolerance and resistance to certain diseases and pests. Also, within a species, different breeds show varying levels of adaptation to thermal stress. It is also generally accepted that *Bos taurus*-type cattle are less adapted to tropical and subtropical hot, and at times also humid, environments than are *B. indicus*-

and Zebu-type cattle. Yousef (1985) attributed the heat adaptability of tropical cattle to, among other factors, their low feed intakes and metabolic rates. In addition, heat loss is increased by a greater surface area, particularly in the region of the dewlap, a larger number of sweat glands, short hair, and fat distribution such that it is inter-muscular or in the hump as in the case of Zebu cattle. These adaptations assist the conductance of heat from the body core to and away from the skin (Ledger, 1959). Comparing *B. taurus* cattle, Sharma et al. (1983) reported that Jerseys were more resistant to heat stress effects on milk production than Holsteins. Sharma et al. (1983) also found reductions in the coefficient of variation of production to be greater in Holsteins than Jerseys, and this ranged from 2.6% units in daily milk production to 6.3% units in daily protein production for Holsteins.

Investigations on the effects of varying ambient temperatures on dairy cows are often limited to studies in which animals were exposed for short periods to constant temperatures in climatic chambers (e.g. Kibler, 1964). With prolonged exposures, adaptations that reduced the effect of a given temperature stress were shown (Kamal et al., 1962). However, Kibler (1964) could not attain complete adaptation to constant high temperatures for 9 weeks in lactating dairy cows. Weldy et al. (1964) concluded that the season in which animals are first brought into the climatic chamber influenced their responses to heat stress.

For lactating cows under commercial production conditions, the effects of heat stress that may be experienced during high day ambient temperatures appear to be ameliorated when night temperatures fall (Akari et al., 1987), thus suggesting short-term tolerance of heat stress. Bitman et al. (1984) proved this phenomenon by showing a diphasic circadian pattern characterized by a high body temperature from midnight to early morning, a decline in midmorning, a rise in afternoon until evening, and a second trough until a rise about midnight. However, Bitman et al. (1984) could not explain the causes of this daily variation of body temperature in the cow. On the other hand, Igono et al. (1992) observed that the lack of a cool night ambient temperature component removes the safety margin that minimizes the negative effects of hot environments.

Berman et al. (1985) calculated a slope of -0.29 to -0.38 MJ/m^2/24 h/°C adaptive changes of tissue and hair conductance relating the non-evaporative heat loss of dairy cows to air temperature. This was similar for mature steers of British breeds (Blaxter and Wainman, 1964), crossbred beef heifers in Canada (Webster et al., 1976), and lactating Holstein and dry Guernsey cows in Missouri (Kibler and Brody, 1952). Berman (1968) reported reductions in metabolic rate from winter to summer of about 20%, which were unassociated with lower productivity in Israeli-Holstein lactating cows and mature heifers exposed to a near natural subtropical climate. This finding suggests that under normal production conditions, metabolic and insulative adaptations to warm climates and their seasonal changes may be sufficient to maintain normal productivity in warm climates (Webster et al., 1976; Weldy et al., 1964). Phenotypic, physiological, and biochemical adaptation mechanisms are explained in Yousef (1985).

Because animals can adapt to hot environmental conditions by gradual acclimation (Prosser and Brown, 1969), it appears logical to assume that high-producing dairy cows acclimate to gradual warming-up during normal summer months. However, if hot conditions are sudden and prolonged, as is often the case in the Mediterranean areas and in some regions of the United States, cows are less likely to acclimatize. Significant decreases in feed intake and resultant drops in milk production punctuate such heat stress conditions.

4. Heat production and heat gain

Heat production of an animal must of necessity be varied to balance heat dissipation if the animal is to maintain normal body temperature. Within the lactating dairy cow, metabolic processes yield energy to sustain life, for synthesis of body tissues, for lactogenesis and milk secretion; energy is also lost in the form of methane, heat in respiratory gases, in feces, and in urine. Yousef (1985) defines HP as a measure of the sum total of energy transformations happening in the animal per unit time. Heat production is directly controlled by the nervous system (Hammel, 1968), by the endocrine system, through modification of appetite and digestive processes, and indirectly by alterations of the activity of respiratory enzymes and protein synthesis (Yousef, 1985). The influence of environmental temperature on feed intake, production, and thermoregulation in the animal greatly affects the rate of heat production (Brody, 1945). Because of their effect on the rate of metabolism, the concentrations of hormones such as thyroxine, triiodothyronine, growth hormone, and glucocorticoids, are closely related to heat production (Yousef and Johnson, 1966). Other factors influencing heat production in mammals include: body size (Brody, 1945), the environment (Salem et al., 1982), animal species and breed, and the availability of feed and water (Graham et al., 1959). Kibler and Brody (1954a,b) noted breed differences between Jersey and Holstein cows in the rate of heat production and dissipation which may be attributed to differences in body size. The temperature gradient between internal organs and external environment is steeper in the smaller Jerseys than in the larger Holstein cows.

4.1. Net energy of maintenance

After summarizing results from calorimetric studies with diets ranging from poor quality forage to all concentrate diets, Blaxter (1961) concluded that the efficiency of use of ME for maintenance was fairly constant. However, the Agricultural Research Council (1980) described variation in the efficiency of use of energy for maintenance (k_m) as a function of the percentage of ME in the diet (Q_m) as: $k_m = 54.6 + 0.30Q_m$. In other studies, Van Es and Nijkamp (1969) concluded that ME was used for milk production at an efficiency of (k_l) 54–58% and that 2.4–2.8 kJ of ME were required for the maintenance of a 500-kg cow (22.9–26.5 kJ of ME/kg$^{0.75}$). Further, Moe et al. (1970, 1971) used multiple regression analyses to derive partial efficiencies of ME use for milk production and BW gain in lactating cows of 64 and 75%, and an efficiency of maternal body gain in non-lactating cows of 60%. Moe et al. (1971, 1972) estimated the efficiency of use of body tissue energy for milk production by cows in early lactation to be 82%. This was after comparing partial regression coefficients representing the amount of ME required for milk production and the amount of dietary ME spared by body tissue loss. In addition, Moe et al. (1972) identified the relationship between diet quality and efficiency of milk production, and expressed dietary energy as net energy (NE) for lactation (NE_l). Maintenance requirements were estimated to be 29.2 and 26.6 kJ of ME or 18.9 and 16.2 kJ of NE_l/kg$^{0.75}$, depending on whether ME intake or milk output was the dependent variable.

Flatt et al. (1965) measured the average fasting HP of non-lactating, non-pregnant dairy cows to be 17.6 kJ/kg$^{0.75}$ following a period of maintenance feeding and concluded that the amount of energy required for maintenance of lactating cows could be described as 17.4 kJ of NE_l/kg$^{0.75}$, and thus suggested that a separate NE term for maintenance (NE_m) was unnecessary. However, Taylor et al. (1986) suggested that individuals and breeds vary in the efficiency with which nutrients (energy) are used for maintenance processes. Ion transport is a major contributor to maintenance energy costs (Milligan and Summers, 1986). Ion transport has been found to be enhanced in the duodenal mucosa of lactating compared to non-lactating cows, although this may be as much the result of altered food consumption as a direct reflection of changed physiological state (McBride and Milligan, 1984). Conventional estimates of the maintenance energy requirements of lactating cows are assumed to be a function of metabolic body size and energy density of the diet, although the Agricultural Research Council (1980) noted that the metabolic rate of milking cows is higher than that of dry animals. This keeps open the possibility that there is indeed variability between individuals in maintenance energy needs.

Although it is impossible to measure separately the maintenance energy requirements and the energy cost of milk production in a lactating animal, Maltz et al. (1982) examined the energy balance of lactating and non-lactating Bedouin goats in relation to maintenance energy during lactation. Maltz et al. (1982) concluded that either the net energetic cost of milk production varies with the level of production or that the energy cost of maintenance increases with increasing milk production or a combination of both. Furthermore, they reported that the goat is a ruminant that neither mobilizes body tissue for milk production at peak production nor deposits tissue energy as lactation declines. This finding appears to validate the linear regression equations used to extrapolate energy requirements to zero production and comparison of the results with measured values.

4.2. Heat increment

Under warm to hot (ambient temperatures of 15 and >25 °C, respectively) conditions, the cow gains heat from solar radiation and from the usual metabolic processes (NE_m and HI). If heat gain exceeds heat loss from radiation, convection, evaporation and conduction, heat is stored and the body temperature rises (Finch, 1986); the animal becomes heat-stressed. At night, when ambient temperatures decrease, heat flow may reverse direction, with stored heat being dissipated from the animal back to the environment and the body temperature may fall. Webster et al. (1976) discussed other heat generation mechanisms including the cost of eating and ruminating, heat produced by fermentation in the rumen (H_f), and the increased heat produced by the tissues of the liver and the gut as the HI. Webster et al. (1975) cited a range in energy costs of eating, 11 J/kJ of ME for grass pellets and 151 J/kJ of ME for fresh grass, and concluded that the energy cost of ruminating could be discounted as a contribution to HI.

Furthermore, Webster et al. (1975) found no differences in HI due to diet source and estimated the H_f in sheep to be 285 J/kJ of digestible energy from forage diets; however, heat production increased exponentially with increasing ME intake. At an intake of 34 kJ of ME/kg$^{0.75}$, heat production in tissues of the gut was 7 kJ/kg$^{0.75}$ per 24 h. Fasting heat production of gut tissues was 4 kJ/kg$^{0.75}$. Therefore, HI due to feeding in the gut was 2.9 kJ/kg$^{0.75}$, of which 1.7 kJ was fermentation heat and 1.2 kJ was aerobic metabolism in gut tissues. Webster et al. (1976) concluded that the processes of ingestion and digestion account for about 25–30% of total HI. Armstrong and Blaxter (1957) ascribed most of the variation in total HI to the nature of substrates made available for metabolism.

4.3. Environment

Environmental temperature influences total energy use in several ways. Young (1976) emphasized that heat stress is described too frequently as temperature alone. Lee's (1965) compilation included (a) environmental variables: temperature, humidity, air movement, radiation, and precipitation; (b) animal characteristics: species, age, sex, breed, metabolic state, coat, acclimatization, nutrition and hydration, disease, and individual variability; and (c) criteria of effect: productivity, growth, reproduction, physiological response, and pathological patterns. This illustrates the complexity of describing and predicting the impact of environmental effects on dairy cattle. However, most metabolic research has been conducted under conditions of 'thermal neutrality' so that environmental effects must be considered in applying such data to extreme conditions, e.g. to animals in thermal stress.

Every interaction that the animal has with its thermal environment involves at least heat exchange. The rate of exchange depends on the ability of the environment to accept heat and water vapor. The flow reverses if ambient temperature is greater than body temperature. This relationship between the animal and its environment determines the degree to which an animal remains in thermal equilibrium with its environment (Finch, 1976). The thermal load of an animal is affected by, among other factors, the animal housing system, shaded or exposed, ventilation, the location of the animal, its social rank, and by changes in position of the dominant animals (Berman et al., 1985). In order for a cow to maintain homeothermy in the environment, the amount of heat she produces or gains from the environment should equal the heat lost to the environment as expressed by the equation:

$$M = \pm K \pm C \pm R + E \tag{4.3.1}$$

where M is the metabolic heat production; K is the heat exchanged by conduction; C is heat exchanged by convection; R is heat exchanged by radiation and E is heat exchanged by evaporation.

5. Heat dissipation mechanisms

To understand the heat dissipation mechanisms of animals, it is important to note that body temperature is relatively constant because of the balance that exists between heat production and heat loss. Heat gain can be expressed as: (heat gained = mass × specific heat × temperature change). Factors that increase heat production over BMR include: exercise or shivering, imperceptible tensing of muscles, chemical increase of metabolic rate, heat increment and disease (fever). Factors decreasing heat loss are an internal shift in blood distribution, a decrease in tissue conductance, or reduction of counter-current heat exchange. On the other hand, heat loss from the animal is enhanced by sweating, panting, a cooler environment, increased skin circulation (vasodilatation), shorter fur insulation, increased sensible water loss, increased radiating surface, and increased air movement or convection.

The animal loses heat by conduction, convection, radiation, evaporation of water, and through expired air. Heat dissipation is shifted from radiation and convection at lower environmental temperatures to vaporization at higher temperatures. Heat lost by the skin depends partly on the temperature gradient between the skin, air and solid objects. Non-evaporative heat loss declines as ambient temperatures rise above the LCT making cows more dependent upon peripheral vasodilatation and water evaporation to enhance heat loss and prevent a rise in body temperature (Berman et al., 1985). Peripheral vasodilatation, however, is unlikely to be a major method of increasing heat dissipation in cattle because of their large body mass. Berman et al. (1985) reported that the maximal rate of water evaporation in lactating cows was 1.5 kg/h, which translates to 4.3 kJ/day. This rate of heat loss is close to the heat production of a dry, non-pregnant 600-kg cow but only about half that produced by a cow producing 30 kg of milk a day. This may explain the low sensitivity of dry cows to high ambient temperatures. The importance of water as a medium for ridding the body of excess heat through sweating and respiration greatly increases as the ambient temperature rises (Richards, 1985).

In cattle under heat load, about 15% of the endogenous heat is lost directly from the body core via the respiratory tract (McDowell et al., 1976). The remainder of the metabolic heat must be transferred to the skin, where it is dissipated either non-evaporatively by radiation, convection and conduction, or evaporatively by sweating. For beef cattle standing in a hot radiant environment, metabolism accounts for about one-third of the total heat load (Finch, 1976), and the ability of animals to remove metabolic heat efficiently is important for maintenance of steady body temperature. The mechanisms of heat transfer from the body core to the periphery of cattle and its dissipation, including breed differences, have been described (Finch, 1986).

5.1. Radiation

The amount of radiant heat absorbed by an object depends not only on the temperature of the object, but also on its color and texture, with dark surfaces radiating and absorbing more heat than light colored surfaces at the same temperature. An animal with a black coat will, therefore, have an absorbance of 1; whereas, a white-coated one will have an absorbance of 0.37 and one with red fur has an absorbance of 0.65 (Cena and Monteith, 1975). Dmi'el et al. (1979) found that direct solar radiation triggered sweating in black Bedouin goats. Furthermore, Dmi'el et al. (1980) reported that the black color of the Bedouin goats was an advantage during cold desert winter mornings. The coat color allows the goat to exploit radiant heat in maintaining body temperature that otherwise would have to be maintained by metabolic energy during a season when pasture is scarce. The disadvantage of the black coat color during the hot summer months is alleviated by insulative properties of the hair as well as by other physiological adaptations to maintain water balance.

Radiant heat transfer between bodies takes place in both directions, and if the bodies are at different temperatures there is a net transfer of heat from the warmer to the cooler body (Esmay, 1969). This net heat transfer involves the loss or gain of heat by the animal through absorption or emission of infrared radiation. Esmay (1969) expressed the net rate of radiant heat transfer (q_r) from one surface at T_1 to another surface at T_2 as:

$$q_r = \delta A_1 F_A F_E (T_1^4 - T_2^4) \qquad (5.1.1)$$

where q_r is the rate of radiant heat transfer; δ is a constant; A_1 is the surface area in cm^2; F_E and F_A are dimensionless factors to account for the emission and absorption characteristics of the two surfaces; T_1

and T_2 are the temperatures of the surfaces in degrees Celsius.

Eq. (5.1.1) may be rewritten to include the numerical value of the Stephan–Boltzmann constant as follows:

$$q_r = 0.173A_1F_AF_E[(T_1/100)^4 - (T_2/100)^4]. \quad (5.1.2)$$

In experiments using artificial radiant heat loads, Stewart and Brody (1954) and Kibler and Brody (1954a) found that cows did not respond to radiation at an ambient temperature of 7.2 °C. However, at temperatures of 21.1 and 26.7 °C, Jersey cows had a mean heat production rate 12–14% lower with maximum radiation load. On the other hand, Holstein cows showed heat production decreases of 26% at 21.1 °C and of 9% at 26.7 °C. In the same experiments, Stewart and Brody (1954) and Kibler and Brody (1954a,b) found that Brahman cows showed little response to radiation insofar as heat production was concerned. The authors concluded that the lack of response by Brahman cows was due to their low heat production rate; therefore, their heat dissipation requirement was not more than half that of the lactating Jerseys and Holsteins.

5.2. Evaporation

Evaporative cooling from the outer surface of cattle is significant. This method of heat dissipation is most efficient in environments where there are low wet-bulb and high dry-bulb temperatures, in other words, hot and dry conditions. The proportion of metabolic heat that is dissipated from an animal's body by evaporation increases with rising environmental temperatures and a decreasing temperature gradient between animal and air. Johnson (1976) showed that differences in the ratio of evaporative cooling to total heat loss (heat produced) is species-variable and that the evaporative ratio of cattle begins to increase markedly at 16.6–18.3 °C. Under thermal stress, cattle increase evaporative heat loss by both panting and sweating, with sweating being quantitatively superior to panting (McLean, 1963). Heat transfer by evaporation is described by the equation:

$$Q_e = k_eA_eV^n(p_s - p_a) \quad (5.2.1)$$

where Q_e is evaporative heat transfer; k_e is the evaporative constant; A_e is the effective evaporative (wet) area; V^n is the air velocity to some power n; p_s is the vapor pressure of water on the animal's surface; p_a is the vapor pressure of water in the air.

It is important to note that evaporative and convective effects on heat loss are not easily separable. As indicated in Eq. (5.2.1), air velocity is one of the important factors influencing evaporative heat transfer. Ittner et al. (1951) reduced skin and body temperatures by increasing the air velocities over pigs and cattle subjected to high ambient temperatures. These findings were pivotal to the development of modern forms of air ventilation to ameliorate heat stress in domestic animals.

5.3. Convection

When cool air comes in contact with a warm body, a layer of air surrounding the surface of the body is heated and rises moving away from the body, carrying with it heat, and thereby cooling the body through the process of convection. On the contrary, if air temperature is greater than skin temperature, then air movement will promote the movement of heat into the animal until air temperature equals skin temperature when transfer of heat ceases. The transfer of heat during respiration is a form of convective heat transfer. Inspired air is adjusted to the body temperature by the time it reaches the trachea (Yousef, 1985). The velocity of air movement affects the rate of convection and anything that resists air movement such as fur in cattle will decrease the rate of heat transfer by convection. The rate of convective heat exchange is described by ASHRAE (1966) as:

$$q_{ev} = hA_{ev}V^n(t_s - t_a) \quad (5.3.1)$$

where q_{ev} is convective heat loss; h is the heat transfer coefficient; A_{ev} is the effective convective surface area; V^n is air velocity to some exponent; $t_s - t_a$ is the difference between the animal's surface temperature and the environmental air temperature.

Esmay (1969) included the velocity factor in the convective coefficient, along with many other physical factors in the equation:

$$q_{ev} = h_{ev}A(t_1 - t_2). \quad (5.3.2)$$

Detailed physical relationships on convection as a way of heat transfer between an animal and its environment are described by Esmay (1969).

5.4. Conduction

The heat flow between two media or bodies in direct contact is described as conductive heat exchange. For dairy cattle, conductive heat exchange is between the animal and its surrounding air environment, and between the animal and any other media, solid or otherwise that the animal may be in direct contact with. When the other media with which the animal is in contact with are either gases or liquid, the conductive heat exchange is further complicated by heat exchange through convection in these media. The flow of heat by conduction depends on the temperature difference, the conductance (or inversely the resistivity) of the medium, and the area of contact (Schmidt-Nielsen, 1964). Esmay (1969) reported a proportional relationship between the bulk density of materials and their conductivity, thus the more dense the material the greater the conductivity or inversely the less the resistance to heat flow. The conductive heat transfer was described by Yousef (1985) in a simple diffusion equation as:

$$K = Ah_c(t_s - t_a) \tag{5.4.1}$$

where K is conductive heat exchange; A is surface area; h_c is thermal conductivity of the material in contact with the skin; t_s is mean skin temperature; t_a is air temperature.

For the high producing dairy cow it is important to know that the magnitude of conductive heat transfer depends on the nature of material in contact with its skin, in particular its thermal conductivity. To alleviate heat stress, utilization of bedding materials with high conductance may facilitate cooling of the animals. From experiments with different bedding materials (wood shavings, sand, ground limestone, shredded paper and rubber mats), Cummins (1998) found that cows had highest preference for ground limestone which had the lowest temperature of 25.9 °C at 25 mm below the surface. This underscores the importance of bedding material selection as part of heat stress abatement strategies. In the standing animal, conductive heat loss is minimal because of the presence of a layer of air against the skin, which means that most of the heat transfer from the animal takes place to air, and air has a poor thermal conductivity (Yousef, 1985). Furthermore, in a standing animal, transfer of heat to the ground only takes place through the feet with a very small area of contact and, in cows, the distance between the blood vessels and the surface is much greater in the feet than it is in the skin. On the other hand, an animal lying on a cool wet surface will have greater conductive heat transfer depending on the thermal conductance of the substrate as well as the temperature gradient and magnitude of the area of contact relative to the total surface area (Eq. (5.4.1)). If air temperature or temperature of the ground on which the animal is lying is greater than skin temperature, then the animal will gain heat by conduction, adding to the metabolic heat load.

6. Responses to heat stress

Life processes of homeotherms, including dairy cows, are adapted for optimum function in their respective thermal neutral environments. Any change in the environmental conditions, as is the case during heat stress, threatens the normal metabolic balance and usually produces a positive feedback once the temperature is above the UCT. In dairy cattle, as milk production increases, metabolic heat production rises with the metabolism of large amounts of nutrients, which makes the high-producing cow more vulnerable to high ambient temperatures and humidity than animals that are less active metabolically. ‘Metabolism and productivity run parallel’ (Brody, 1945). High-producing cows are affected more than low-producing cows because the TNZ shifts downward as milk production, feed intake, and heat production increase (Coppock et al., 1982), assuming that the heat dissipation mechanisms of both types of cows are similar. Continued genetic progress suggests that milk production will increase and so will the detrimental effects of heat stress on the modern dairy cow. Heat stress increases loss of body fluid due to sweating and panting. If this continues unchecked, the fluid loss can reach a critical level, becoming a threat to thermoregulation and cardiovascular function (Silanikove, 1994).

The general homeostatic responses to thermal stress in mammals include reduction in fecal and urinary water losses, reduction in feed intake and production, and increased sweating, as well as initial increases in respiratory rates and heart rates, which would slow down if heat stress persists. In response to stress, the dairy cow sets physical, biochemical, and physiological processes into play to try and counteract the negative effects of heat stress and maintain thermal equilibrium. Most of the adjustments made by the cow involve dissipating heat to the environment and reducing the production of metabolic heat.

6.1. Physical responses

Responses of the cow to temperatures above the TNZ are varied. These include raised respiration rates and rectal temperature (Omar et al., 1996), panting, drooling, reduced heart rates, and profuse sweating (Blazquez et al., 1994), decreased feed intake (National Research Council, 1989) as well as reduced milk production (Abdel-Bary et al., 1992).

Physical responses to heat stress in dairy cows appear to be breed-specific (Finch, 1986), with the *B. indicus* and other tropical breeds being less responsive to thermal stress than *B. taurus* cattle. The differences in response to heat stress between cattle breeds are attributed to varying levels of adaptability to hot environments. Sharma et al. (1983) showed that, within *B. taurus* dairy cattle breeds, the Jersey was less sensitive to thermal stress than the Holstein-Friesian.

6.1.1. Sweating

In dairy cows, there are two types of sweating that occur: both are appreciably involved in heat dissipation. The first type is insensible sweating or perspiration that leaves the body at all times, unless the relative humidity is 100%. Another type, thermal sweating, occurs as the principle evaporative cooling mechanism of the cow when ambient temperatures rise. The heat required to convert water into vapor is referred to as the latent heat of vaporization. The vaporization of 1 ml of water requires 2.43 J and this is the amount of heat lost when 1 ml of sweat evaporates from the skin.

The proportion of metabolic heat that is dissipated from the cow by evaporation increases with rising environmental temperatures and a decreasing temperature gradient between the animal and air. The morphology and functioning of the apocrine sweat glands of cattle during hot climatic conditions has been extensively investigated (Montgomery et al., 1984). Blazquez et al. (1994) reported that increased blood flow to the skin is positively correlated to the sweating rate.

Earlier, Kibler and Brody (1952) found similar sweating rates for *B. taurus* and *B. indicus* breeds; however, Allen (1962) showed that *B. indicus* and Zebu cattle had significantly higher sweating rates than breeds from temperate regions. Ferguson and Dowling (1955) and Allen (1962) ascribed elevated sweating rates of *B. indicus* and Zebu cattle to their higher density of sweat glands. Schmidt-Nielsen (1964) reported that as the environmental temperature rose, *B. taurus* cattle showed an appreciable increase in evaporation between 15 and 20 °C, with a maximum rate of evaporation being reached before 30 °C. On the contrary, Brahman cows (*B. indicus*) had initially lower evaporation rates, but rapid evaporation rates occurred when temperatures were between 25 and 30 °C, and continued rising up to 40 °C. Cattle in temperate and tropical regions possess the same type of sweat glands, one to each hair follicle (Findlay and Yang, 1950). However, tropical breeds have a higher density of hair follicles ($1698/\mathrm{cm}^2$ for Zebu) than is the case in *B. taurus* breeds ($1064/\mathrm{cm}^2$ for Shorthorn) (Dowling, 1955). Furthermore, Dowling (1955) reported that Zebu have sweat glands that are located much closer to the skin surface than is the case in temperate breeds of cattle. Blazquez et al. (1994) did not attach significance to the number of sweat glands per unit area or to their individual size, but more to the product that these sweat glands produce.

The measurement of sweating rate is difficult and results have been varied. Robertshaw and Vercoe (1980) reported a twofold increase in the rate of skin moisture loss (up to 77 $\mathrm{g/m^2/h}$) from the scrotum after exposure to a temperature of 40 °C. Blazquez et al. (1994) measured a fivefold increase in the rate of skin moisture loss (up to 279 $\mathrm{g/m^2/h}$) from the scrotum at 36.2 °C. Finch (1986) found that the sweating rates of *B. indicus* increased exponentially with rises in body temperature; whereas, in *B.*

taurus, the sweating rates tended to plateau after an initial increase. Within *B. taurus* breeds, Singh and Newton (1978) found higher ($P<0.05$) sweating rates in Ayrshire calves than in Guernsey calves and suggested that Ayrshire calves were more capable of acclimation to hot weather than Guernsey calves.

6.1.2. Rectal temperature

Rectal temperature is an indicator of thermal balance and may be used to assess the adversity of the thermal environment which can affect the growth, lactation, and reproduction of dairy cows (Johnson, 1980). A rise of 1 °C or less in rectal temperature is enough to reduce performance in most livestock species (McDowell et al., 1976), which makes body temperature a sensitive indicator of physiological response to heat stress in the cow because it is nearly constant under normal conditions. Shalit et al. (1991) recorded rectal temperatures of lactating cows as 0.9 °C higher than in pre-partum cows, although environmental conditions were similar. Their explanation was that lactating dairy cows appeared to be more thermo-labile than non-lactating ones because of a reduced capacity of lactating cows to stabilize their plasma volume and concentration within a narrow range.

Furthermore, Berman et al. (1985) confirmed the findings of Gonsalez et al. (1978) for humans, Young et al. (1959) for dogs and Wilson et al. (1978) for rats, that during thermal equilibrium the rectal temperature of high-producing dairy cows is independent of air temperature, but related to energy metabolism. Bianca (1964) showed that the ingestion of 51 l of 14 °C water decreased rectal, skin, and subcutaneous temperatures 1.7 °C in oxen exposed to 40 °C in a climatic chamber. In feeding experiments, Hormer et al. (1954) measured slightly lower rectal temperatures for fasted cattle than for the same animal when normally fed. In studies on diurnal temperature cycles and feed intake of Holstein dairy cows, Scott et al. (1983) concluded that the initiation of night cooling of the animals at a time when their rectal temperature was highest was most beneficial to the maintenance of a thermal neutral plasma T_4 level. Scott et al. (1983) found a negative relationship between average plasma T_4 concentration (T_4, in ng per ml) and average rectal temperature (T_r, in degrees Celsius: $T_4 = 278.42 - 5.37T_r$, $r^2 = 0.67$ ($P < 0.01$)). They also reported negative relationships between feed intake (FI, in kilograms per day) and both average THI and average dry bulb temperature (T_d, in degrees Celsius): $FI = 101 - 5.4THI$, $r^2 = -0.66$ ($P<0.05$), and $FI = 57.3 - 5.7T_d$, $r^2 = -0.66$ ($P<0.05$), respectively, in non-lactating Holstein dairy cows. These results suggested that night cooling might be an effective natural method to alleviate thermoregulatory limitations of a hot climate on optimal animal performance.

It appears that there are notable differences between breeds in their abilities to regulate rectal temperature: the mean rectal temperature is higher in *B. taurus* than in *B. indicus* cattle (Finch, 1986) and, as a result, *B. taurus* cattle are more sensitive to heat stress than their *B. indicus* counterparts.

6.1.3. Blood gases

The maintenance of blood pH is high on the list of homeostatic priorities and pH depends primarily on the relative concentrations of carbonic acid and base bicarbonate in blood (Coppock et al., 1982). From a physiological standpoint, Coppock et al. (1982) measured body temperature and respiration rate, milk production and composition, and blood components that reflect the acid–base balance and found that cows fed $NaHCO_3$ and no supplemental NaCl had lower body temperatures than the other groups.

Under heat stress, four conditions may result. Metabolic acidosis and metabolic alkalosis involve bicarbonate; respiratory acidosis and respiratory alkalosis are related to the partial pressure of carbon dioxide (p_{CO_2}) (Dale and Brody, 1954). A pH below 7.4 stimulates respiration (Diven, 1975); whereas, a higher pH decreases it. A p_{CO_2} greater than 40 mmHg stimulates respiration; whereas, a lower p_{CO_2} inhibits it.

In chamber experiments, cows subjected to heat stress had a higher blood pH during hot hours compared to those in a thermal neutral environment (Schneider et al., 1988). Bianca and Findlay (1962), described reduced blood CO_2 combining capacity and the resultant higher blood pH as respiratory alkalosis. Schneider et al. (1988) reported an apparent renal compensation to the alkalosis during heat stress which was indicated by increased urine pH of cows in hot environments compared to when the cows were in a cooler environment. Bianca (1965) attributed the increased urine pH to increased bicarbonate (HCO_3^-) excretion into the urine and showed that urine pH increased even during mild heat stress. Masero and Siegel (1977) described the HCO_3^- buffering mechanism, in which HCO_3^- and p_{CO_2} are relatively constant at a ratio of 20:1, as the most important buffering system in blood. Thermally induced hyperventilation decreases p_{CO_2} and, to maintain the ratio at 20:1 and counter alkalosis, HCO_3^- is secreted by the kidney. This results in decreased blood HCO_3^- and raised urine pH. Correction for the urinary alkalosis is effected by renal excretion of H^+, which results in resorption of HCO_3^- into the blood (Masero and Siegel, 1977). In addition, heat stress raises the partial pressure of blood oxygen (p_{O_2}) due to increased alveolar ventilation (Hales and Findlay, 1968) and raises mean plasma (Schneider et al., 1988) as well as urine creatinine concentrations (Thompson, 1973), suggesting muscle catabolism.

6.1.4. Respiration rate

There is no evidence of breed differences in the respiratory response to low temperatures, but at high temperatures, Kibler and Brody (1954a) showed that Jersey cows had much higher respiration rates than Holsteins, which they attributed to the Jersey's better ability to dissipate heat compared to Holsteins. High ambient temperatures induce physiological adjustments, including increased respiration rate (Coppock et al., 1982). Johnston et al. (1959) reported increases from 20 breaths/min under cool conditions to 100 breaths or more per minute at 32 °C and above. In studies involving high-producing dairy cows in a subtropical environment, Berman et al. (1985) found that the respiratory frequency started rising above 50–60 breaths/min at ambient temperatures higher than 25 °C.

The importance of relative humidity in the study of heat stress was demonstrated by a decline in milk production between 32 °C with 20% relative humidity (RH) and 32 °C with 45% RH (Johnson and Vanjonack, 1976). This difference in RH reduced respiratory and surface evaporation, which resulted in a rise in rectal temperature, reducing feed intake and milk production.

Lanham et al. (1986) showed that 20 min after drinking 10 °C or 28 °C water, respiratory frequency of lactating Holstein cows decreased from 17 to 38.6 breaths/min and from 3.4 to 52.4 breaths/min ($P < 0.05$), respectively. Milam et al. (1985) also measured the respiratory frequency before watering (88.9 and 87.7) and after watering (81.2 and 83.8); however, decreases in respiration rates (7.6 and 4.0) were similar ($P > 0.05$) at the same water temperatures of 10 and 28 °C.

6.1.5. Heart rate

Kibler and Brody (1951) showed that the pulse rate decreased in *B. taurus* cattle subjected to chronic, moderate heat stress. Singh and Newton (1978) reported a decline in the heart rate (HR) of 2–3-month-old male *B. taurus* calves when the temperatures were raised from 18 to 40.5 °C at 50% RH. The mean HR of 114.5/min fell to 110.5/min on day 1 in the climate chamber, and continued to fall to 95/min by day 14 of exposure. Contrary to expectations, Richards (1985) measured an increase of the HR ($P < 0.01$) of lactating Friesian cows after a diurnal exposure of the cows to high ambient temperature (38 °C at an RH of 80% for up to 7 h/day) for 3 weeks. This treatment was subsequent to a 3-week period of normal temperatures (14–21 °C and RH 60–70%) for 17 h/day.

A reduced HR is more typical in heat-stressed cows as it is associated with a reduced rate of HP as a response to high environmental temperatures. Richards (1985) explained this deviation as being attributed to the fact that the cows were not acclimatized to tropical conditions and they were exposed to daily acute bouts of heat stress for the first time, and that increased HR was consistent with a stress response. This was in agreement with the report of Bianca (1959) that, in cattle, the HR increases during short-term exposure to heat and decreases with long-term exposure. Huhnke and Monty (1976) did not find any significant variation in the HR of pre- and post-parturient Holstein-Friesian cows during the cool and hot weather seasons in Arizona. Singh and Bhattacharyya (1990) concluded that the pulse rate of livestock was very variable at different test temperatures and among different genetic groups. Newer data indicate that heat stress can cause either dilution, concentration, or have no effect on blood plasma volume, and the effect of heat stress on blood volume affects steroid hormone concentrations in blood (Johnson et al., 1991; Elvinger et al., 1992).

Muller and Botha (1993) compared the effect of summer climatic conditions in South Africa on different heat tolerance indicators in primiparous Friesian and Jersey cows. They reported higher ($P < 0.05$) HR for Friesians than for Jerseys at 15:00 and 17:00 h measurements. Muller and Botha (1993) concluded that HR was not influenced to the same extent as rectal temperature and respiratory rate by increasing ambient temperatures.

Huhnke and Monty (1976) noted that the average HR of post-parturient cows during cool weather (74.5/min, minimal rate; 79.2/min, maximal rate) was lower ($P < 0.01$) than the rates of pre-parturient cows during cool weather (92.3/min, minimal rate; 98.5/min maximal rate). The significantly higher HR of pre-parturient cows exposed to cool weather when compared to HR of post-parturient cows under similar climatic conditions could be explained by the cardiovascular stress of pregnancy because of increased blood flow through the placenta. This increase was masked during hot weather.

6.2. Metabolic responses

Christopherson and Kennedy (1983) and Lu (1989) reported reduced metabolism in cattle under heat stress, which they found to be associated with reduced thyroid hormone secretion and gut motility, resulting in increased gut fill. Mitra et al. (1972) found plasma growth hormone concentration and growth hormone secretion rate to decline with hot temperatures (35 °C). Igono et al. (1988) showed that the concentrations of growth hormone in the milks of low-, medium-, and high-producing cows declined when the THI exceeded 70 and suggested a suppressed production of growth hormone in order to lower metabolic heat production. McGuire et al. (1991) found that plasma growth hormone reductions that occurred with heat stressed cows did not occur in thermoneutral conditions for cows fed amounts that were similar to those consumed during heat stress. Also working with lactating cows, Johnson et al. (1988) measured declines in thyroid hormones triiodothyronine (T_3) and thyroxine (T_4) in response to heat stress, which they attributed to attempts to reduce metabolic heat production in the cow. Earlier, Alvarez and Johnson (1973) attributed higher concentrations of epinephrine and norepinephrine in blood plasma to heat stress in dairy cows. The literature suggests that cows respond to heat stress by engaging homeostatic processes to maintain homeothermy.

6.2.1. Mineral metabolism

Leach (1979) used the term cation–anion balance to refer to physiologic interrelationships among Na, K, and Cl, whose importance had been recognized by poultry nutritionists. The role of sulfate in the cation–anion balance must also be recognized. Insufficient quantities of dietary sulfur limit the synthesis of sulfur-containing amino acids (e.g. methionine, cysteine) and that way reduce milk production (Clark et al., 1978). Bouchard and Conrad (1973) found increased dry matter (DM) digestibility from 67% in the basal diet to 69.4% after adding potassium, sodium, or magnesium sulfate to diets of lactating cows. Furthermore, Bouchard and Conrad (1973, 1974) reported maximal DM digestibility by cows when dietary sulfur was 0.15% on a DM basis (53 mg/kg of BW/day), and suggested that cows consuming less than maximum feed intake would benefit from raised dietary sulfur levels of 0.18, 0.19, and 0.20% for cows consuming 90, 80, and 70% of their maximum feed intake, respectively. Heat stress reduces feed intake in lactating dairy cows, and therefore, increased dietary sulfur should raise DM digestibility and provide sufficient sulfur for microbial synthesis of the otherwise milk production-limiting sulfur-containing amino acids.

Leach (1979) reported that the main adverse effect of an acid–base imbalance comes from the acidogenic action of excess Cl. This effect could, however, be reversed by the alkalogenic nature of Na and K, and these three elements are instrumental in maintaining acid–base balance. In the posterior segment of the intestine and in the kidney, Cl is absorbed in excess of Na with a simultaneous secretion of bicarbonate (Coppock et al., 1982). Metabolic acidosis may occur if available Na in these regions is reduced, possibly increasing Cl absorption, draining HCO_3^- and increasing Cl in the plasma. Metabolic alkalosis may result from a reciprocal process. Another possibility is a H^+–Na^+ and Cl^-–HCO_3^- exchange. Excess Na^+ may cause a greater H^+ depletion in plasma leading to alkalosis; whereas, excess Cl^- has a negative effect on HCO_3^- leading to acidosis. Further alterations in renal absorption of Na and HCO_3^- from dietary changes are other possible explanations of changes in blood acid–base balance (Coppock et al., 1982).

The effects of dietary Na, K, and Cl balance on acid–base physiology and production in lactating dairy cows was investigated by Tucker et al. (1988). The DM intake (DMI) and the pH of rumen fluid, blood, and urine increased linearly with increasing dietary cation–anion balance [Na + K–Cl, (DCAB)], suggesting a beneficial effect from feeding a cationic diet during lactation. Tucker et al. (1988) used diets formulated to provide DCAB of −10, 0, +10, or +20 meq/kg of DM. Electrolyte concentrations, in particular Na and K, are reduced in the rumen fluid of heat-stressed dairy cattle because of the increased loss of Na in urine and K in sweat. Schneider et al. (1988) reported an increased secretion of K in the sweat of heat-stressed dairy cows. Shalit et al. (1991), Maltz and Silanikove (1996) and Silanikove et al. (1997) found that the retention mechanisms for Na^+, K^+ and Cl^-, the main ions involved in sweat, were more efficient in summer than in winter. These researchers concluded that the greater part of the elevated summer milk-free water balance (about 20 kg/day) is devoted to evaporative water loss. Irrespective of this fact, cows that calve in summer do not maintain plasma Na^+, K^+ and Cl^- homeostasis and plasma volume (Maltz et al., 1994).

El-Nouty et al. (1980) noted that urinary Na output increased during heat stress. Several studies have shown significant increases in the milk production of heat-stressed dairy cows when fed higher than recommended (National Research Council, 1989) concentrations of Na and K through dietary addition of $NaHCO_3$ and KCl (Silanikove et al., 1997). Schneider et al. (1988), however, found no differences in DMI (21.3 vs. 21.0 kg/day) or milk production (18.3 vs. 17.4 kg/day). In addition, these authors found no differences in solid turnover rates for cows consuming the high mineral diet (average K intake of 411 g/day; average Cl intake of 394 g/day) compared with the basal diet. For the treatment group, water intake was higher (82.2 vs. 70.2 l/day; $P < 0.01$), and the rumen fluid dilution rates were faster ($P < 0.01$). In the same experiment, Schneider et al. (1988) found that ruminal fluid from cows consuming a high mineral diet had lower concentrations of volatile fatty acids (VFA) ($P < 0.05$), with trends towards higher molar percentages of acetate, lower molar percentages of propionate and a higher acetate to propionate ratio. These results agreed with Rogers et al. (1982), that Na and K exert alkalogenic effects and Cl an acidogenic effect on the acid–base balance (Cohen et al., 1972).

Escobosa et al. (1984) fed dairy cows a diet containing 1.67% Cl during moderate heat stress and reported lowered blood pH, p_{CO_2} and urine pH compared with a control diet (0.34% Cl), which is consistent with Schneider et al. (1988). Furthermore, Schneider et al. (1988) measured higher concentrations of K in the rumen, but Na concentrations were not increased by a diet high in minerals. This is consistent with the observations of Greene et al. (1983). Requirements for specific nutrients for milk production, such as Na and K, appear to differ during thermal stress compared to thermal neutral conditions (Beede et al., 1985). It appears necessary to establish prediction equations for nutrient requirements especially of Na, K, and Cl fed to high-producing dairy cows in different productive phases, but more importantly in early lactation, and at varying degrees of thermal stress. This is seen in the light of the finding in poultry nutrition (Mongin, 1980) that plasma bicarbonate concentration was linearly related to the sum of Na + K–Cl meq/100 g of air-dry diet. In addition, Mongin (1980) demonstrated a marked dependence of blood pH on dietary chloride and suggested that ideally Na + K–Cl should equal 250 ± 30 meq/kg of air dry diet for growing poultry. Analogous calculations for the DCAB of dairy cows can be found in Tucker et al. (1988) and Waterman et al. (1991).

The addition of $NaHCO_3$ to the diet of dairy cows increased ruminal pH, altered rumen fermentation and, in proper amounts, alleviated the low-fat milk syndrome, that often occurs in lactating dairy cows consuming high concentrate diets (Muller and Kilmer, 1979). It was found that $NaHCO_3$ acts by increasing ruminal pH, which in turn increases the ratio of acetate to propionate (Esdale and Satter, 1972). Furthermore, it appears that sodium bicarbonate and mineral salts with no buffering capacity, such as NaCl, increase the fractional dilution rate of rumen fluid. This in turn increases the molar percentage of acetate and decreases the molar percentage of propionate in cows fed a high concentrate diet (Rogers and Davis, 1980). Sodium bicarbonate also increases ruminal pH, thereby establishing a more favorable environment for fiber digestion (Rogers et al., 1982). The literature shows that mineral salts influence several aspects of nutrient digestion, rumen fermentation patterns, and several physiological processes, whether the cows are under thermal stress or not.

6.2.2. Water metabolism

The total body water is estimated to range between 75 and 81% of BW for lactating dairy cows. Among environmental factors considered to be important in controlling water intake in lactating dairy cows are temperature, humidity, DMI, nature of the diet, and milk production (Murphy et al., 1982). High producing cows consume more DM than low producing ones, with DMI and water consumption being positively correlated (MacFarlane and Howard, 1972). Heat stress simultaneously influences both energy and water metabolism (Silanikove, 1992), and increases plasma and extracellular fluid volume in proportion to the thermoregulatory requirement of the stressed cow. Cows under thermal stress tend to have increased water content in the rumen as a result of an accelerated water turnover rate (Silanikove, 1989). This agrees with the finding that sheep exposed to a hot environment ingested a volume of water far above the minimal needed for intermediate metabolism and for evaporation (Blaxter et al., 1959). More data on the factors affecting water absorption through the ruminal epithelium can be found in Dobson (1984), and the interrelationships between food intake, osmolality, salivation and water balance in the rumen have also been reviewed (Carter and Grovum, 1990).

Today, the water intakes of cows producing 41.5 kg of milk/day under thermoneutral conditions are about 135 kg/day. This is more than double that ingested by a cow in early lactation producing 29.4 kg/day of milk of a comparable composition 30 years ago (Flatt et al., 1969). In addition, the evaporative water loss of cows today (46 kg/day) exceeds the total amount of milk-free water balance (39.5 kg/day) available for metabolic and evaporative processes in the cows studied by Flatt et al. (1969).

After allowing for fecal water loss, the high-producing dairy cow at peak production in a temperate environment with water turnover of 135 kg/day is left with 99 kg of water/day circulating through its body to satisfy metabolic and thermoregulatory processes (Silanikove et al., 1997). This water reaches various tissues and organs as it circulates through the plasma volume. Assuming a plasma volume of 7% of BW, a plasma volume of 38.5 l is calculated for the cow (Woodford et al., 1984). This means that water circulating through the plasma volume is over 2.5 times its total volume, implying that the plasma volume is exchanged 2.5 times daily as compared to 1.7 times per day for cows producing 25.7 kg of milk/day as described by Woodford et al. (1984). The calculation reveals a problem of maintaining a steady plasma volume in the cow and suggests that either the efficiency of water transfer through the biological membranes has increased dramatically (by about 50%) or the plasma volume has been raised, or both. Either of these possibilities has a significant thermoregulatory advantage.

Water loss from an animal is a continuous process; taking place all the time and increasing during heat stress because of additional evaporative water loss. In contrast, water intake by the animal is episodic. In order to maintain volume homeostasis of body water compartments, there must be a ‘water reservoir’ from which water is continuously withdrawn to compensate for losses in other compartments. Work with desert ruminants that drank water once per day suggests that the gastrointestinal tract is this water reservoir (Shkolnik et al., 1980).

Water intake remains fairly stable during the precalving period and maintains blood plasma electrolyte concentrations constant (Maltz et al., 1994). Water intake of a high producing dairy cow under heat stress doubles at the second week post-partum (Shalit et al., 1991). In the seventh week post-partum, the amount of water ingested increases only slightly; however, the drinking pattern changes drastically. Large fluctuations in drinking volumes throughout day and night, thus challenging the physiological ability of the animal to maintain the gastrointestinal tract homeostasis of volume and solutes, are seen. During this period, substantial fluctuations in blood plasma electrolyte concentrations and volume were recorded, suggesting one of two possibilities. Either the regulatory mechanisms to maintain gastrointestinal volume and solutes stability collapsed because of the need to transfer water between compartments or the cow developed a resistance to blood plasma fluctuations in concentrations and volume, thereby removing the need to regulate the stability of the water reservoir. Both possibilities have significant thermoregulatory consequences. The former possibility is supported by the fact that milk production declined slightly during the latter period when fluctuations in water intake occurred and blood plasma homeostatic capacity improved through electrolyte supplementation during this period (Silanikove et al., 1998).

6.2.3. Digestive tract

High environmental temperatures may affect the rumen microorganisms that synthesize the B-vitamins, amino acids, and fatty acids on which the nutrition of ruminants largely depends. Available data suggest that rumination is depressed during dehydration and heat stress (Aganga et al., 1990). Also during heat stress, blood flow to rumen epithelium is depressed (Hales et al., 1984). Heat stress decreased reticular motility and rumination (Attenberry and Johnson, 1968); whereas, the volume of digesta in the rumen of beef cows, Bedouin goats (Silanikove and Tadmore, 1989) and swamp buffalo (Chiaiyabutr et al., 1987) increased. Silanikove (1992) postulated that heat stress increased the water content of digesta in the rumen and its volume, thereby increasing its capacity to serve as a water reservoir to counterbalance the effect of heat stress on rumen motility.

Mishra et al. (1970) measured higher concentrations of lactic acid and lower ruminal pH in heat-stressed cattle, which may imply that a high lactic acid concentration and lower ruminal pH might be involved in inhibiting rumen motility during heat stress. Beede and Collier (1986) concluded that rumen function during heat stress may be altered by pituitary effects on basal metabolism, such as via reduced somatotropin and thyroid hormones.

In ruminants, digesta fill contributes up to one-quarter of the BW, most of it in the rumen where the ratio between DM and water is about 1:10 (Silanikove, 1994). Heat stress in highly productive cattle appears to be partially related to an increase in gut fill (Miller et al., 1974).

Kelly et al. (1967) observed that heat stress reduced the concentration of VFA in the rumen of cattle, a response which would not be expected to cause the inhibition of reticulo-rumen motility associated with heat stress. There is no clarity on the involvement of gastrointestinal hormones and peptidergic neurons in mediating the effect of temperature on gastrointestinal motility. Grovum (1981) noted that some of the gastrointestinal hormones that influence motility also affect feed intake in ruminants. The large number of biologically active compounds produced in the gut that may influence motility and passage makes this area very complex (Bloom, 1978).

The fractional rate of digesta passage in the gastrointestinal tract of heat-stressed animals is slower than that of animals in a thermal neutral environment, which reflects reduced intake, ruminal activity and motility (Silanikove, 1992).

Schneider et al. (1988) reported faster fractional dilution (10.9 vs. 8.6%/h) and passage (3.6 vs. 2.8%/h) rates in thermal neutral compared with heat-stressed lactating cows, respectively. However, Croom et al. (1982) showed that the salts of saliva, mainly $NaHCO_3$, and mineral salts increased ruminal fluid dilution rates and feed intake in steers and dairy cows. When the dilution rate increases, the growth rate of ruminal-microbes increases and the fraction of fermented substrate needed for microbial maintenance decreases (Isaacson et al., 1975). This increases the efficiency of fermentation. Increased passage of digesta in heat-stressed cows fed greater quantities of mineral salts may increase feed consumption and milk production, thus alleviating the major negative production-related responses to heat stress. Increased milk production by heat-stressed cows fed higher than recommended (National Research Council, 1989) concentrations of dietary Na and K have been widely reported (West et al., 1987).

During heat stress, the VFA concentration would be reduced, decreasing inhibition of the gastric center and increasing the motility of the reticulo-rumen. After holding feed intake constant in hot and thermal neutral environments, Niles et al. (1980) measured lower ruminal VFA concentrations in the hot environment, as well as reduced amplitude and frequency of ruminal contractions. This agreed with the results of Schneider et al. (1988) working with lactating cows in natural and chamber heat-stressed environments. The fractional rates of ruminal fluid dilution and solid digesta passage, and total VFA concentrations were lower in the heat-stressed cows compared to cows in a thermal neutral environment.

6.2.4. Nutrient digestibility

Changes in the thermal environment can induce alterations in the activity and function of the digestive system, which are independent of changes in feed intake (Christopherson and Kennedy, 1983). In heat-stressed animals, National Research Council (1989) noted that the digestibility of feed components increased due to reduced intake. Graham et al. (1959) working with sheep and Blaxter and Wainman (1961) experimenting with steers reported a positive relationship between environmental temperature and energy digestibility. Further studies confirmed the influence of environmental temperature on digestibility in sheep and cattle (Christopherson, 1976). In contrast, Guerrini (1981) found conflicting results that may be attributed to temperature treatments with variations in feed intake and the possible selective refusal of some diet components, all of which can introduce variability into digestion experiments. Information on the exact nature of the relationship between temperature and digestion is scant.

Robertshaw (1981) suggested that a slower rate of digesta passage and longer mean retention time accounted for slightly higher digestibility coefficients during heat stress. Wiestra and Christopherson (1976) agreed that the digestibility of DM in the whole tract was directly related to the total mean retention time. The slower rate of digesta passage in animals exposed to heat loads is a result of depressed feed intake. Warren et al. (1974) reported a mean retention time 18% greater at 32 vs. 18 °C, when feed intake was kept equal among steers by feeding through the rumen fistula. In contrast, studies in hot environments have not confirmed depressed fractional passage rate or rumen activity via control of feed intake. Warren et al. (1974) found increased feed digestibility as a result of heat stress.

The influence of animal insulation on the response to temperature would suggest that digestibility may be related to metabolism. In experiments where sheep were fed 1420 g of bromegrass pellet DM/day and were exposed to cold temperatures or subjected to alterations in thyroid status by thyroidectomy, treatment with exogenous T_3, or both, Christopherson (1976) found an inverse relationship between oxygen consumption and digestibility. Although a positive relationship between digestibility, especially of fiber components, and ambient temperatures has been reported (Lu, 1989), high temperatures had little effect on diet digestibility in dairy cows (McDowell et al., 1976) and goats (Lu, 1989). An evaluation of available information shows that there is an increase in digestibility in response to high temperature that may be explained by reduced DMI and a prolonged retention of feed in the gastrointestinal tract.

6.3. Production responses

Thermal stress can negatively impact the performance of intensively managed livestock in the southern US and in other subtropical and tropical regions of the world (Beede and Collier, 1986). For lactating dairy cows, ambient temperatures above 25 °C are associated with lower feed intake, drops in daily milk production, and reduced metabolic rate (Berman, 1968), and decreased conception rate (McDowell et al., 1976). These adjustments are strategies to maintain normal body temperature (Beede and Collier, 1986).

Physical protection, genetic development, and nutritional dietary manipulation are three fundamental management practices that have been proposed to ameliorate the effects of heat stress. Extensive data on the effect of heat stress on production responses, physiology, and general health of dairy cattle have been reported (Beede and Collier, 1986). Although the magnitude may vary depending on the cows used and other experimental procedures, the available data show a general trend of responses to heat stress by lactating cattle. Heat-stressed dairy cows in chamber experiments consumed less feed (13.6 vs. 18.4 kg/day; $P<0.01$), more water (86.0 vs. 81.9 l/day;

$P < 0.01$) and produced less milk (16.5 vs. 20.0 kg/day; $P < 0.01$) than cows in a thermal neutral environment (Schneider et al., 1988).

6.3.1. Water intake

Water and macro-mineral needs, influenced heavily by demands to maintain homeostasis and homeothermy, are altered for lactating dairy cows during heat stress (Beede and Collier, 1986). Milk is about 87% water, and contains large concentrations of the electrolytes Na, K, and Cl; therefore, lactating dairy cows have large turnover of water and these electrolytes (Shalit et al., 1991). High-producing dairy cows have increased water intakes and, in heat stress, consume even more water. This is so because highly productive animals have faster dehydration rates (Maltz et al., 1984), brought about by higher rates of water turnover. Richards (1985) observed a transitory increase in BW when lactating Friesian cows were exposed to high daytime temperatures and interpreted this as a temporary rapid ingestion of water to increase total body water. This increase in body water is useful because the high specific heat of water allows the cow to store a great deal of heat during the day and dissipate it during the cool night, much like the camel (Schmidt-Nielsen, 1964). Thompson et al. (1949) showed that the water intakes of individual cows varied considerably when they were exposed to temperatures above 22 °C; however, many studies show significant positive correlation between water intake and ambient temperature (National Research Council, 1989). Furthermore, it is apparent that the temperature of drinking water may influence the quantities drunk and milk production (Anderson, 1985). Anderson (1985) observed the highest water intakes and milk productions from dairy cows when 17 °C water was offered. Close to the finding of Anderson (1985) in Sweden, Ittner et al. (1951) in the Imperial Valley of California reported that beef cattle increased weight gains when given 18.3 °C drinking water compared with 31.2 °C water in summer.

In contrast, Anderson (1985) offered chilled (10 °C) and ambient temperature water (28 °C) during heat stress and found that drinking water temperature did not affect ($P > 0.05$) water consumption, although Holstein cows drank less chilled water, which is consistent with the data of Lanham et al. (1986). Adjusted mean water consumptions in the study of Milam et al. (1985) were 10.5 and 16.1 l/day for 10 and 28 °C water, respectively. This was much lower than the 24.8 and 31.0 l/day with the same temperatures reported by Lanham et al. (1986).

Murphy et al. (1982) restricted a multiple regression analysis to the two variables identified by Little and Shaw (1978), and obtained the relationship $\mathrm{WI} = 22.96 + 2.38$ (standard error $0.275) \times \mathrm{DMI} + 0.64$ $(0.179) \times \mathrm{PROD}$ ($P < 0.0001$). In this equation, WI is water intake in l/day, DMI in kg/day, and PROD is milk production in kg/day. Furthermore, Murphy et al. (1982) calculated through stepwise regression of all independent variables the equation that: $\mathrm{WI} = 15.99 + 1.58\ (0.271) \times \mathrm{DMI} + 0.90\ (0.157) \times \mathrm{PROD} + 0.05\ (0.023) \times \mathrm{SODIN} + 1.20\ (0.106) \times \mathrm{TMIN}$ ($P < 0.0001$). In this equation, TMIN is the weekly mean minimum temperature in degrees Celsius; SODIN is sodium intake in grams per day and the other factors are similar to the first equation. Little and Shaw (1978) found that the daily water intake was correlated ($P < 0.001$) to daily DMI ($r = 0.58$) and to milk production ($r = 0.50$), but not to the DM content of the feed, BW, or mean air temperature. The relationship between DM and water intakes was found to vary with the composition of the diet, in particular the protein, Na, and K content (Agricultural Research Council, 1980). In addition, Silanikove and Tadmore (1989) restricted water availability to beef cows to once every 24, 48, or 72 h, and measured reductions in resting salivary flow rate as well as in voluntary feed intake of 40, 60, and 80%, respectively. These results underscore the relationship between water intake and voluntary feed intake. Variations in feed or water intake led to proportional changes in the other variable and reduced feed intakes decrease metabolic rate and, consequently, lower water losses (More and Siebert, 1983). It is important to note that the amount of saliva secreted appears to depend on the quality and quantity of feed consumed (Brosh et al., 1988). Detailed interrelationships among water intake, other feed constituents, and heat stress have been reviewed (Murphy, 1992; Silanikove, 1992).

6.3.2. Feed intake

Feed intake in lactating cows begins to decline at ambient temperatures of 25–26 °C and drops more rapidly above 30 °C (National Research Council, 1989). At 40 °C, dietary intake may decline by as much as 40% (National Research Council, 1989). Heat stress causes the rostral cooling center of the hypothalamus to stimulate the medial satiety center which inhibits the lateral appetite center, resulting in reduced dietary intake and consequently lower milk production (Albright and Alliston, 1972). Animals in a highly productive state, such as high-producing dairy cows, have feed intakes and metabolic rates that may be two to four times higher than at maintenance (National Research Council, 1989). Heat stress in such high producing lactating dairy cows results in dramatic reductions in roughage intake and rumination (Collier et al., 1982). The reduction in appetite under heat stress is a result of elevated body temperature and may be related to gut fill (Silanikove, 1992). Decreased roughage intake contributes to decreased VFA production and may lead to alterations in the ratio of acetate and propionate. In addition, rumen pH is depressed during heat stress (Collier et al., 1982). In contrast, ruminants adapted to hot environments are able to maintain their appetite under heat stress at near maintenance or during moderate growth (Brosh et al., 1988). In chamber experiments, Schneider et al. (1988) found that heat-stressed cows changed their feeding pattern and ate when temperatures were cooler. In temperature stress experiments with lactating cows, Wayman et al. (1962) showed that the major decrease in milk production at high ambient temperatures is a result of reduced feed intake. Using rumen-fistulated lactating cows, Wayman et al. (1962) demonstrated that the drop in milk production due to heat stress could be reduced by placing feed rejected due to thermal stress directly into the rumen. A decrease ($P<0.05$) in the efficiency of energy utilization for milk production when cows were under heat stress was reported.

6.3.3. *Milk production*

Climatic factors such as air temperature, solar radiation, relative humidity, air flow and their interactions, often limit animal performance (Sharma et al., 1983). Quantifying direct environmental effects on milk production is difficult as milk production is also strongly affected by other factors such as nutritional management (Fuquay, 1981), that may or may not be directly linked to environmental factors. Thatcher (1974) and Johnson (1976), however, reported declines in the productions of milk and fat as a direct result of high environmental temperatures. This may be because heat stress has negative effects on the secretory function of the udder (Silanikove, 1992). McDowell et al. (1976) suggested that milk production is reduced 15%, accompanied by a 35% decrease in the efficiency of energy utilization for productive purposes, when a lactating Holstein cow is transferred from an air temperature of 18 to 30 °C. Milk fat, solids-not-fat, and milk protein percentage decreased 39.7, 18.9 and 16.9%. In addition, Johnson (1976) attributed 3–10% of the variance in lactation milk production to climatic factors. Differences in the physiological responses of cattle to the form and duration of heat stress have been reported and differences have also been noted in productive responses. Bianca (1965) measured a 33% reduction in milk production by breeds of cows from temperate climates exposed continuously to high (35 °C) ambient temperatures. However, cows maintained under similar temperatures during the day but at <25 °C at night did not decrease milk production beyond that normally expected under temperate conditions (Richards, 1985).

The point on the lactation curve at which the cow experiences heat stress is also important for the total lactation yield. Cows are less able to cope with heat stress during early lactation. Heat stress at the initiation of lactation negatively impacts the total milk production. Furthermore, Sharma et al. (1983) concluded that climatic conditions appeared to have maximum influence during the first 60 days of lactation. This early lactation period is when high-producing cows are in negative energy balance and make up for the deficit by mobilizing body reserves. Catabolic processes are associated with metabolic heat production over and above that already induced by high nutrient intake.

Under Mediterranean climatic conditions, summer calvers produce less milk per lactation than winter calvers (Barash et al., 1996). Summer temperatures in the Mediterranean region generally are above the TNZ of dairy cows and result in heat stress.

6.3.4. *Health*

For a variety of reasons, the incidence of health problems in livestock, including dairy cows, increases during warm summer months. Vectors and other disease-causing agents thrive better under warm to hot and humid environmental conditions. In tropical locations, tick and internal parasite populations explode during summer, forcing farmers to dip and drench their livestock more frequently than during the cool winter months. Other than parasitic problems during warm months, it is apparent that heat stress itself can directly and adversely affect the health of the dairy cow.

Using data from dairy herds, DuBois and Williams (1980) calculated that 24% of cows (79 parturitions) that calved during the warm season of May through September had retained placenta and developed postpartum metritis, compared to 12% (98 paturitions) for the rest of the year when temperatures were lower. This difference ($P < 0.05$) was wholly attributed to the effects of heat stress on the dairy cows during the warm months. Furthermore, DuBois and Williams (1980) found a difference ($P < 0.0005$) in the gestation length (273 vs. 279 days) of cows having retained placenta and postpartum metritis than of cows not exhibiting these symptoms. Retained placenta and postpartum metritis occur with early parturition (Wagner et al., 1974) and are of major economic significance for dairy producers. Collins and Weiner (1968) reported that heat stress caused a variety of neuroendocrine changes that may contribute to the shortening of the gestation period. Pavlicek et al. (1989) reported that dairy cows developed 11% more ketosis during hot summer months than in the cooler season; they attributed this to the negative influence of heat stress on dairy cows. Although literature on the effects of heat stress on the health of dairy cows is scant, it seems logical to postulate that the influence of thermal stress on the physiological functions of the high producing cow may trigger clinical or sub-clinical health conditions.

6.3.5. Reproduction

Cavestany et al. (1985) determined the relationship between ambient temperature and breeding efficiency and demonstrated that seasonal high environmental temperatures were associated with low breeding efficiency due to a variety of factors. High summer temperature above the thermoneutral zone of cattle drastically reduced conception rate and presumably increased embryonic loss (Gwazdauskas et al., 1981). Berman et al. (1985) reported reductions in thermoregulatory ability in the face of heat stress as a result of selection for milk production, which magnifies the seasonal depression in fertility caused by heat stress (Al-Katanani et al., 1998). Nebel et al. (1997) found that Holsteins in estrus during the summer have 4.5 mounts per estrus versus 8.6 for those in winter. Wilson et al. (1998) indicated that heat stress caused a reduction in the peripheral concentrations of estradiol-17β at estrus. On the other hand, Wolfenson et al. (1995) reported that heat stress caused an increase in peripheral concentrations of estradiol-17β between day 1 and 4 of the estrus cycle and a reduction from day 4 through 8 and 11 through 21 of the estrus cycle.

Badinga et al. (1993) found that heat stress beginning on the day of ovulation reduced the diameter and volume of the dominant follicle on day 8 of the estrus cycle. Wolfenson et al. (1997) found that heat stress from day 3 to 5 of the estrus cycle increased androstenedione and reduced estradiol-17β concentrations in the follicular fluid of the dominant follicle collected. Hansen and Arechiga (1999) ascribed the physical lethargy produced by heat stress and poor detection of estrus as major reasons for reduced expression of estrus on one hand and reduced numbers of cows eligible for embryo transfer on the other. In addition, Hansen (1997) reported that the deterioration of bull fertility caused by heat stress was another cause of reduced fertility during summer in hot regions.

In artificial insemination studies, Stott et al. (1972) identified the first 4–6 days post-insemination as the most critical. However, Ingraham et al. (1974) claimed that for optimal conception rate, heat stress must be minimized at least 12 days prior to breeding. Heat stress also adversely affected the ovum and sperm in the reproductive tract and early embryo development (Burfening and Ulberg, 1968), and may alter the hormonal balance of the dam (Stott et al., 1972; Thatcher, 1974). Sugiyama (1999) reported that heat shock of maturing bovine oocytes in culture can lead to reduced protein synthesis, fertilization rate, and subsequent developmental competence. Furthermore, Sugiyama (1999) found that exposure of bovine embryos flushed from superovulated heifers at day 6 or 7 of pregnancy to heat shock in culture reduced cell number.

7. Conclusions

Hot weather reduces milk production in cows with high genetic merit for milk production. Strategies to alleviate metabolic and environmental heat loads in early lactation need to be researched and developed. Earlier studies showed that diets with high concentrate and minimum fiber reduced heat stress in lactating dairy cows because the ME from high concentrate diets is used with greater efficiency (less HI) than the ME from high forage diets. Recent advances in animal nutrition, including the feeding of ruminally-protected fats and protected proteins are among other endeavors to reduce metabolic heat production and supply the correct profile of nutrients to high producing cows in early lactation. An adequate supply of nutrients must also include well-balanced mixture of dietary minerals, especially of Na, K, Cl, and SO_4^{2-}. These play a pivotal role in the thermal physiology of the cow. Analysis of milk production data from the last 55 years reveals that milk production per cow has increased over threefold. This is in response to advances in animal nutrition, in technology, and in biotechnology as well as genetic progress for milk production. Using these facts as a basis, it is apparent that genetic selection and other variables enhancing milk production may have resulted in adjustments in factors important to lactation and nutritional physiology of the dairy cow. One such factor, important especially in hot environments, is the thermoregulatory ability and capacity of modern cows. It is important to quantify thermoregulatory capabilities, and the physiological effects of heat stress on high-producing cows in modern dairies. Such empirical data are prerequisites for improving nutrition, fine tuning nutrient supply, and adjusting the management of high merit cows, so that they can express their true genetic potential for milk production.

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