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Heat stress in dairy cattle: Impacts on productivity, physiological responses and mitigation strategies a comprehensive review

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Abstract

Heat stress represents a critical environmental constraint on dairy production systems, particularly under the intensifying effects of climate change, and exerts profound impacts on animal physiology, productivity, and health. It disrupts thermal homeostasis, leading to a cascade of physiological and metabolic alterations that adversely affect feed intake, milk yield, and milk composition. A primary response to elevated thermal load is a reduction in dry matter intake, which directly contributes to decreased milk production and lower milk protein concentration, while effects on milk fat content and feed efficiency remain comparatively variable. The severity of heat stress is commonly evaluated using the temperature-humidity index (THI), with values above approximately 70 associated with significant declines in performance. Notably, the impact of heat stress is not always immediate, as delayed reductions in milk yield and compositional traits are frequently observed, reflecting complex temporal interactions between environmental exposure and biological responses. Additionally, heat stress impairs thermoregulatory mechanisms, as indicated by increased respiration rate, heart rate, and rectal temperature, prompting both behavioral and physiological adaptations aimed at maintaining homeothermy. Advances in precision livestock technologies, including the application of machine learning approaches integrating environmental and physiological data, have enhanced the accuracy of heat stress detection and monitoring. Effective mitigation strategies are therefore essential to minimize production losses, with cooling interventions such as evaporative adiabatic systems combined with forced ventilation proving particularly effective in facilitating heat dissipation. A comprehensive understanding of these mechanisms and responses is fundamental for developing adaptive management strategies that ensure sustainable dairy production and improved animal welfare under conditions of thermal stress.

Keywords: Heat stress, dairy cattle, Temperature-Humidity Index (THI), milk production thermoregulation, cooling strategies

1. Introduction

The progressive rise in global temperatures and the increasing frequency of extreme climatic events, including heatwaves, have intensified concerns regarding the sustainability of dairy production systems worldwide (Kemp et al., 2022; Lee et al., 2023) ^[43, 48]. Heat stress (HS), resulting from the combined influence of environmental factors such as ambient temperature, relative humidity, solar radiation, and wind speed, disrupts the thermal equilibrium of dairy cattle and imposes substantial constraints on productivity, reproduction, and animal welfare (Cartwright et al., 2022; Chauhan et al., 2023) ^[17, 20]. This challenge is particularly pronounced in high-producing dairy breeds such as Holstein cows, which have been genetically selected for elevated milk yield under temperate conditions and exhibit reduced adaptability to hot environments (Baëta, 2010) ^[4].

Dairy cows inherently generate significant metabolic heat due to maintenance requirements and the energetic demands of milk synthesis, which predisposes them to thermal imbalance when environmental heat load exceeds their capacity for heat dissipation (Coppock, 1985; Purwanto et al., 2009) ^[24, 67]. The severity of thermal stress is commonly quantified using the Temperature-Humidity Index (THI), a widely adopted indicator that integrates ambient

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temperature and relative humidity and correlates well with physiological parameters such as respiration rate and core body temperature (Yan et al., 2021; Habeeb et al., 2018) ^[33, 96]. Although THI provides a practical measure of environmental stress, its predictive capability is influenced by the formulation used and does not fully account for individual variability or physiological responses (Bohmanova et al., 2007) ^[13]. To overcome these limitations, alternative indices such as the Heat Load Index (HLI) have been developed, incorporating additional environmental and physiological variables; however, their applicability in extensive systems remains constrained by data availability and spatial variability (Islam et al., 2021) ^[37].

When THI exceeds critical thresholds, dairy cows fail to maintain thermal homeostasis, leading to a cascade of physiological and behavioral responses aimed at dissipating excess heat. These responses include increased respiration rate, elevated heart rate, reduced feed intake, increased water consumption, and behavioral modifications such as seeking shade and reducing activity (Damasceno, 2020) ^[27]. While these adaptive mechanisms are essential for survival, they impose significant energetic costs and result in the reallocation of nutrients away from productive processes. Consequently, heat stress is associated with reductions in dry matter intake, milk yield, and alterations in milk composition, particularly protein concentration (Becker et al., 2020) ^[7]. Importantly, declines in feed intake and milk production do not always occur proportionally, suggesting that heat stress may also influence metabolic efficiency and nutrient partitioning (Wheelock et al., 2010) ^[90]. Variability in feed efficiency responses under heat stress conditions has been reported, with some studies indicating reductions due to increased maintenance energy requirements (Karimi et al., 2015) ^[42], while others report stable or improved efficiency under certain conditions (Rungruang et al., 2014) ^[71].

Beyond its immediate effects on production, heat stress exerts profound impacts on reproductive performance and animal health. Elevated thermal load has been associated with reduced estrus expression, decreased conception rates, prolonged calving intervals, and increased embryonic mortality, thereby significantly compromising reproductive efficiency and farm profitability (Cartwright et al., 2023; Burhans, 2022) ^[14, 16]. Additionally, heat stress increases susceptibility to metabolic and infectious diseases, further exacerbating production losses. The magnitude of these effects is influenced by multiple factors, including the intensity and duration of heat exposure, stage of lactation, and parity of the animal (Tao et al., 2020) ^[83].

Notably, the effects of heat stress are not always immediate; delayed responses have been widely reported, with peak declines in milk yield and compositional traits occurring several days after exposure, reflecting cumulative physiological strain (Chapman et al., 2023) ^[19]. These lagged effects highlight the complexity of thermal stress responses and underscore the importance of temporal dynamics in evaluating production outcomes. In extensive production systems, particularly pasture-based systems, assessing the impact of heat stress is further complicated by variability in environmental conditions, management practices, and breed characteristics, as well as limitations in continuous data collection (Scerri et al., 2023) ^[74]. Technological advancements, such as automated in-field weighing systems, have improved the ability to monitor animal performance in real time, thereby enhancing the understanding of heat stress impacts in such systems (Hasan et al., 2024b) ^[35].

In contrast, intensive dairy production systems provide controlled or semi-controlled environments that facilitate detailed monitoring of physiological and production responses, enabling the identification of critical thermal thresholds and response mechanisms (Koch et al., 2016) ^[46]. These systems serve as valuable models for understanding heat stress dynamics and developing mitigation strategies applicable across diverse production contexts. Recent advances in precision livestock farming, including the integration of machine learning techniques, have further enhanced the detection and prediction of heat stress by combining environmental, physiological, and behavioral data (Inadagbo, 2024) ^[36]. Such approaches enable proactive management interventions, improving the effectiveness of heat stress mitigation.

To alleviate the adverse effects of heat stress, various management and environmental interventions have been developed, including housing modifications, ventilation systems, evaporative cooling, and nutritional adjustments (Leso, 2020) ^[49]. However, the adoption of these strategies is often constrained by economic considerations, particularly in regions experiencing frequent and prolonged heat stress conditions. Given the increasing global prevalence of thermal stress, there is a critical need for a comprehensive understanding of its multifaceted impacts on dairy cattle, including production, reproduction, and health, as well as the development of effective and economically viable mitigation strategies.

Therefore, this review aims to synthesize current knowledge on the effects of heat stress on dairy cow productivity, physiological responses, and adaptive mechanisms, while also evaluating the role of environmental indices, emerging detection technologies, and mitigation strategies in improving resilience and sustainability of dairy production systems under changing climatic conditions.

2. Review methodology

A comprehensive literature search was conducted using Google Scholar, supplemented by relevant institutional databases and organizational reports, to ensure the inclusion of both peer-reviewed and grey literature on heat stress in dairy cattle. Multiple keyword combinations were employed, including “heat stress in dairy cows,” “mitigation strategies,” “cooling systems,” “Temperature-Humidity Index (THI),” and “milk production under heat stress,” without strict geographical or temporal restrictions. The final dataset comprised 128 peer-reviewed journal articles, 5 credible web sources, and 2 institutional reports, with the majority published after 2000, reflecting increased research focus in this domain. Inclusion criteria required that selected studies provide evidence-based insights into at least one of the following aspects: physiological, productive, reproductive, or immunological impacts of heat stress. Non-English publications, anecdotal evidence, and sources lacking direct relevance to the review objectives were excluded through a systematic screening process.

3. Thermoregulation

Dairy cattle are homeothermic animals, possessing the inherent capacity to regulate and maintain a relatively constant core body temperature despite fluctuations in environmental conditions and metabolic activity (Baëta, 2010) ^[4]. This thermoregulatory ability is essential for sustaining physiological stability and optimizing productive performance. Under conditions where ambient temperature

remains within the thermoneutral zone, animals can maintain thermal balance without expending additional energy on heat dissipation mechanisms, thereby allowing maximal expression of productive potential such as milk synthesis (Tinôco, 2001) ^[85].

Heat stress arises **כאשר** environmental temperatures exceed the upper critical limit of this thermoneutral zone, resulting in an imbalance between internal heat production and heat loss. Under such conditions, dairy cows activate a range of physiological and behavioral thermoregulatory responses aimed at dissipating excess body heat and preserving homeothermy. These responses include increased peripheral blood flow, enhanced evaporative heat loss through respiration and sweating, and behavioral adaptations such as reduced activity and increased water intake (Ouellet, 2021) ^[58].

As ambient temperature continues to rise beyond the critical threshold, the efficiency of these mechanisms declines, leading to an accumulation of body heat and elevated core body temperature. This condition imposes additional metabolic demands on the animal, as energy is diverted from productive functions toward maintenance of thermal balance. Consequently, prolonged exposure to heat stress not only disrupts physiological equilibrium but also compromises productivity, health, and overall animal welfare.

3.1 Thermoneutral Zone, LCT, and UCT

The Thermoneutral Zone (TNZ) represents the range of ambient temperatures within which dairy cattle maintain a stable metabolic rate and regulate body temperature primarily through non-evaporative physical processes, without expending additional energy. Within this zone, animals can sustain optimal physiological function and productivity. The Lower Critical Temperature (LCT) defines the threshold below which animals must increase metabolic heat production to maintain thermal equilibrium, whereas the Upper Critical Temperature (UCT) represents the point beyond which heat dissipation mechanisms become insufficient, leading to an elevation in metabolic rate and activation of evaporative cooling processes (Kumar et al., 2018) ^[47].

The combined influence of environmental temperature and relative humidity is commonly assessed using the Temperature-Humidity Index (THI), which serves as a reliable indicator of heat stress severity. In general, THI values below 75 are considered to impose minimal or no stress on ruminants, while values exceeding 79 indicate the onset of thermal discomfort, and levels above 84 represent severe heat stress conditions. Maintenance of core body temperature within the normal physiological range of approximately 38.4 °C to 38.7 °C is essential for proper metabolic functioning in dairy cattle. However, under hot and humid conditions, the efficiency of heat dissipation is markedly reduced, increasing the risk of thermal stress. Conversely, animals are better able to tolerate higher ambient temperatures when relative humidity is low, due to more effective evaporative heat loss (Basak et al., 2013) ^[15].

3.2 Heat dissipation mechanisms in ruminants

In ruminants, body heat is generated primarily through metabolic processes, including digestion, physical activity, and basal physiological functions. These processes produce endogenous heat via chemical and mechanical pathways, which must be effectively dissipated to maintain thermal equilibrium (Kumar et al., 2018) ^[47]. Heat exchange between the animal and its environment occurs through both sensible

and latent mechanisms. Sensible heat loss involves conduction, convection, and radiation, where heat is transferred along a temperature gradient between the animal's body and the surrounding environment (Shephard and Maloney, 2023) ^[77].

The efficiency of sensible heat loss is highly dependent on the difference between body surface temperature and ambient conditions. As environmental temperature approaches or exceeds body temperature, these mechanisms become progressively ineffective, necessitating reliance on evaporative heat loss. Evaporation, therefore, becomes the primary mode of heat dissipation under heat stress conditions, occurring mainly through sweating and respiratory processes. Sweating contributes approximately 70% of total evaporative heat loss, while panting or increased respiratory activity accounts for the remaining proportion (Dairy Australia, 2023) ^[26]. The effectiveness of this process depends on environmental humidity, as high relative humidity limits evaporative cooling efficiency. Breed differences are also evident, with *Bos indicus* (zebu) cattle exhibiting greater sweating capacity and superior adaptation to hot climates compared to *Bos taurus* breeds.

Several environmental and animal-related factors influence the efficiency of heat dissipation and increase susceptibility to heat stress. Key environmental constraints include elevated air temperature, high relative humidity, intense solar radiation, inadequate ventilation, and prolonged exposure to hot conditions. Additionally, limited access to shade and water further exacerbates thermal load. Animal-specific factors such as coat color, hair length, and body composition also play a critical role; darker-coated and heavily insulated animals absorb more heat and dissipate it less efficiently. Physiological status further modulates heat stress vulnerability, with growing, pregnant, and lactating animals generating greater metabolic heat, thereby increasing their susceptibility. Similarly, animals with higher body fat content exhibit reduced heat dissipation capacity and are more prone to thermal stress. Collectively, these factors interact to influence the animal's ability to maintain thermal balance under challenging environmental conditions.

3.3 Impacts of heat stress: physiological responses

Heat stress induces a wide range of physiological and behavioral responses in dairy cattle aimed at maintaining thermal balance, although these adaptations often compromise productivity and health. Animals exposed to excessive heat exhibit characteristic behavioral signs such as drooling, panting, tongue protrusion, and extension of the neck, reflecting attempts to enhance heat dissipation. Due to their high metabolic heat production associated with lactation, dairy cows are particularly susceptible to thermal stress (Carabaño et al., 2017) ^[15]. In addition to endogenous heat generation, cattle are also exposed to external thermal loads from solar radiation and environmental heat, further increasing their body heat burden. Under normal conditions, body temperature follows a circadian rhythm with minor fluctuations; however, this pattern becomes disrupted during periods of heat stress (Piccione and Refinetti, 2003) ^[65].

As environmental temperature rises beyond critical levels, thermoregulatory mechanisms such as sweating and panting become increasingly active to maintain core body temperature within the normal range of approximately 38-39.2 °C (Collier et al., 2012) ^[23]. Elevated Temperature-Humidity Index (THI) levels intensify panting activity, which may lead to respiratory alkalosis and subsequent disturbances in rumen

pH balance (Carabaño, 2017) ^[15]. Respiration rate is a key indicator of heat stress, with values exceeding 60 breaths per minute signaling thermal discomfort in dairy cows, and rates potentially rising to as high as 150 breaths per minute under severe stress conditions (Berman, 2005) ^[8]. Heart rate also increases in response to elevated temperature, with reports indicating an approximate 15% rise when ambient temperature exceeds 30 °C (Kim et al., 2022) ^[45].

Behavioral adaptations serve as early indicators of heat stress, including increased water intake, reduced feed consumption, seeking shade, and decreased lying time. Cows tend to remain standing for longer periods to increase body surface area exposed to air, thereby facilitating heat loss; however, prolonged standing is associated with reduced milk yield and increased risk of health disorders (Schutz et al., 2011) ^[75]. Water intake significantly increases under heat stress conditions, often doubling compared to normal levels, with high-producing dairy cows consuming up to 200 liters per day (Atrian and Shahryar, 2012; Giannone et al., 2023) ^[3, 31].

Feeding behavior is also markedly altered, with animals shifting feed intake to cooler periods of the day such as early morning, evening, and night. Feed intake begins to decline at temperatures around 25-26 °C and may decrease by up to 40% at extreme temperatures approaching 40 °C (Rhoads et al., 2013) ^[70]. Reduced feed intake contributes to a negative energy balance and weight loss, while also serving as a physiological mechanism to limit metabolic heat production. Additionally, rumination activity declines under high THI conditions, with a greater proportion occurring during cooler nighttime hours (Soriani et al., 2013) ^[79]. In severe cases of heat stress, core body temperature may exceed 41 °C, and clinical signs such as frothy nasal or oral discharge may indicate advanced physiological distress, including pulmonary complications (Vermunt and Tranter, 2010) ^[86].

3.4 Impact of heat stress on production

Heat stress exerts a pronounced negative effect on milk production in dairy cattle (Table 1), with high-yielding animals being particularly vulnerable due to their elevated metabolic heat load. Dairy cows typically begin to experience thermal stress when ambient temperatures exceed

approximately 25 °C, resulting in a marked decline in dry matter intake, often ranging between 20% and 40% (Correa-Calderon et al., 2004) ^[25]. This reduction in nutrient intake, combined with increased maintenance energy demands under heat stress conditions, contributes to a progressive decline in milk yield.

The relationship between thermal stress and milk production is strongly associated with the Temperature-Humidity Index (THI). Studies have demonstrated that for each unit increase in THI, milk yield decreases by approximately 0.69 kg in Holstein Friesian cows and 0.45 kg in Jersey cows (West et al., 2003) ^[89]. In addition to quantity, heat stress also adversely affects milk quality. Alterations in milk composition have been reported, particularly in fatty acid profiles, when heat-stressed cows are compared to those maintained under thermoneutral conditions (Liu et al., 2017) ^[51].

Heat stress is associated with significant reductions in key milk constituents, including protein and fat. For instance, milk protein concentration has been observed to decline from 3.02 g/100 g to 2.89 g/100 g, while milk fat decreases from 3.46 g/100 g to 3.17 g/100 g when THI exceeds 75 (Abeni et al., 1993). Furthermore, short-term exposure to elevated temperatures can result in substantial changes in milk lipid composition, including a marked reduction in polar lipid content within a few days of heat exposure (Liu et al., 2017) ^[51]. Additional components such as solids-not-fat (SNF), milk urea nitrogen, immunoglobulins (IgG, IgA), casein, and lactalbumin are also negatively affected under heat stress conditions, reflecting impaired mammary gland function and increased oxidative stress, often accompanied by elevated somatic cell counts (Chen et al., 2023) ^[21].

Beyond direct effects on milk synthesis, heat stress also influences feed quality and nutrient utilization. Elevated temperatures can reduce the digestibility of forage by limiting the breakdown of structural carbohydrates such as lignin, thereby decreasing feed efficiency. This contributes to a negative energy balance, loss of body condition, and further declines in productive performance. Collectively, these effects highlight the substantial impact of heat stress on both the quantity and quality of milk production in dairy systems.

Table 1: Effects of Temperature-Humidity Index (THI) on Dairy Cattle Production and Milk Composition

Parameter	<68 (No Stress)	68-71 (Mild Stress)	72-76 (Moderate Stress)	≥77 (Severe Stress)	THI > Threshold (Per Unit Increase)
Daily Milk Yield Change (kg/cow/day)	0.089	0.04	-0.023	-0.123	Up to -0.249
Milk Fat Content (%)	3.51	3.46	3.42	3.37	-0.006
Milk Protein Content (%)	3.19	3.15	3.13	3.09	-0.008
Milk Urea Concentration (mg/dL)	10.9	10.4	10.8	11	Increases
Solids-Not-Fat (SNF, %)	8.98	8.97	8.96	8.79	Decreases
Somatic Cell Count (SCC)	Normal (baseline)	Begins to rise	Elevated; critical threshold ≥72	Markedly elevated; critical ≥78	↑ SCC (~36% increase)
Dry Matter Intake (DMI) Change	Baseline	↓ ~2-3%	↓ ~4-5%	↓ ~4.13% per THI unit	-4.13% per THI unit
References	Oliveira et al., 2025; Yadav et al., 2025; Besteiro et al., 2025; Chen et al., 2024 ^[11, 22, 57, 95]				

3.5 Effect of heat stress on reproduction

Heat stress represents a major constraint to reproductive efficiency in dairy cattle, inducing a cascade of physiological, endocrine, and behavioral disruptions that collectively impair fertility. At the herd level, elevated thermal load is associated with an increased incidence of anestrus and repeat breeding, while effects on abortion and dystocia appear comparatively limited. However, postpartum complications, including

retained placenta, tend to increase under moderate heat stress conditions, suggesting that thermal stress primarily disrupts ovarian function and postpartum reproductive physiology (Wolfenson and Roth, 2018; Sumi et al., 2022) ^[80, 92]. Fertility declines markedly when the temperature-humidity index (THI) exceeds 72, particularly when animals are exposed to heat stress before or during the breeding period (Dash et al., 2016) ^[29].

Behavioral expression of estrus is significantly suppressed under heat stress. Compared to thermoneutral conditions, where cows exhibit frequent mounting and standing behavior, heat-stressed animals display minimal estrus activity, especially during daytime hours (Szalai et al., 2025) ^[81]. These behavioral changes are closely linked to endocrine alterations, including reduced progesterone concentrations and premature regression of the corpus luteum (Nanas et al., 2021) ^[56]. Heat stress also impairs ovarian function by suppressing Luteinizing Hormone (LH) secretion and reducing estradiol synthesis, resulting in inadequate follicular development and diminished ovarian activity. Consequently, conception rates decline sharply, from approximately 40-60% under thermoneutral conditions to as low as 10-20% during periods of heat stress, with a large proportion of estrus events remaining undetected (Rutledge, 2001) ^[72].

Follicular dynamics are further altered under heat stress, characterized by an increased proportion of large follicles and delayed establishment of follicular dominance, which disrupts normal reproductive timing (Wolfenson et al., 1995) ^[94]. Elevated progesterone levels during the late luteal phase may prolong the estrous cycle and interfere with synchronization protocols (Lucy, 2001) ^[52]. Additionally, increased secretion of stress-related hormones such as adrenocorticotrophic hormone (ACTH) and cortisol suppresses estradiol-mediated sexual behavior, further reducing the likelihood of successful mating (Das et al., 2016) ^[28]. The efficiency of artificial insemination is also compromised, with success rates declining significantly when body temperature exceeds 40 °C (Pereira et al., 2013) ^[63].

Heat stress adversely affects embryonic development through multiple mechanisms, including reduced interferon-tau production, increased oxidative stress, and altered expression of apoptosis-related genes, all of which contribute to reduced embryo viability (Wolfenson et al., 2000) ^[93]. As a result, conception rates are significantly lower in heat-stressed animals compared to those maintained under thermoneutral conditions (Khan et al., 2013) ^[44]. Furthermore, the majority of embryonic losses occur during the early stages of gestation, often before day 42, due to compromised uterine environment and disrupted endocrine regulation (Sammad et al., 2020) ^[73]. Male fertility is also negatively influenced by heat stress, with detrimental effects observed on sperm quality, including reduced motility, impaired acrosomal integrity, increased abnormal spermatozoa, and elevated levels of oxidative damage (Lyrio et al., 2023) ^[53]. Although some degree of seasonal adaptation may occur, prolonged exposure to high temperatures continues to impair reproductive performance. Additionally, heat stress disrupts the hypothalamic-pituitary-gonadal axis, altering hormonal regulation and further compromising reproductive outcomes.

Overall, the cumulative impact of heat stress on both male and female reproductive systems leads to substantial reductions in fertility. Pregnancy rates decline progressively with increasing THI, with reported reductions of approximately 1.03% per unit increase above a threshold of 72 (Liu et al., 2019) ^[50]. Prolonged exposure to heat stress also affects fetal development and extends calving intervals, ultimately reducing overall herd productivity and efficiency (Kaewlamun et al., 2011) ^[41]. These findings underscore the critical need for effective heat stress mitigation strategies to sustain reproductive performance in dairy production systems.

4. Molecular mechanisms and physiological effects of heat stress

Heat stress disrupts cellular homeostasis in dairy cattle primarily through oxidative imbalance and activation of the Hypothalamic-Pituitary-Adrenal (HPA) axis, both of which interact synergistically to exacerbate physiological dysfunction (West, 2003) ^[89]. At the cellular level, elevated temperatures impair mitochondrial electron transport chain activity, leading to excessive generation of Reactive Oxygen Species (ROS), including superoxide anions and hydrogen peroxide, often increasing by two- to threefold (Marquez-Acevedo et al., 2023) ^[55]. This overproduction overwhelms endogenous antioxidant defense systems, such as superoxide dismutase (SOD) and catalase (CAT), resulting in oxidative stress and cellular damage (Zeng et al., 2022) ^[97].

In response to thermal stress, the endocrine system initiates a coordinated adaptive response aimed at maintaining internal homeostasis. Acute exposure triggers the release of hormones such as antidiuretic hormone, prolactin, glucocorticoids, and catecholamines, which collectively function to stabilize blood pressure, regulate fluid balance, and support circulatory adjustments (Sejian et al., 2013) ^[76]. Conversely, aldosterone secretion tends to decline, impairing sodium retention and contributing to challenges in maintaining electrolyte balance. With prolonged exposure, the endocrine response shifts toward energy conservation, characterized by reduced secretion of growth hormone, thyroxine, and glucocorticoids, thereby negatively affecting metabolic rate, growth, and stress resilience (Das et al., 2016) ^[28].

Heat stress also induces significant alterations in metabolic processes. Animals experience increased evaporative heat loss through sweating and panting, leading to depletion of water and essential electrolytes. Prolactin plays an important role beyond lactation by regulating sodium and potassium balance under dehydrating conditions. However, sustained heat exposure results in reduced feed intake, impaired glucose and lipid metabolism, restricted fat mobilization, and the development of negative energy balance, forcing animals to utilize body reserves for maintenance (Rhoads et al., 2009; Sammad et al., 2020) ^[69, 73]. Notably, despite elevated circulating insulin levels, peripheral insulin resistance develops, further compromising metabolic efficiency and productivity (Baumgard and Rhoads, 2013) ^[70].

Reproductive endocrine function is also adversely affected. In males, prolonged heat exposure reduces testosterone levels, leading to impaired spermatogenesis and decreased fertility (Pérez-Crespo et al., 2008) ^[64]. In females, heat stress disrupts follicular development, lowers conception rates, and increases embryonic loss (Ozawa et al., 2005) ^[59]. Additionally, heat stress interferes with cellular processes such as protein synthesis, enzyme activity, and membrane integrity, resulting in decreased levels of erythropoietin, hemoglobin, and packed cell volume, along with reduced activity of key metabolic enzymes (Sonna, 2002) ^[79].

Hormonal profiles undergo marked changes under heat stress. For instance, growth hormone concentrations decline significantly, while prolactin levels increase to support mammary function. Thyroid hormones, particularly triiodothyronine (T3), decrease, reflecting a reduction in metabolic activity (Farooq et al., 2010) ^[30]. Elevated cortisol levels further indicate activation of the stress response and contribute to metabolic and immune alterations. Heat stress also modifies rumen fermentation patterns, favoring increased production of propionate and butyrate relative to acetate,

thereby disrupting normal energy metabolism (Chaidanya et al., 2017) ^[18].

At the cellular defense level, heat shock proteins (HSP70 and HSP90) are upregulated to stabilize and repair damaged proteins, providing a protective mechanism against thermal injury (Volloch and Rits, 1999) ^[88]. However, under prolonged or severe stress, these protective systems may become insufficient. Compromise of intestinal barrier integrity allows translocation of endotoxins into circulation, further aggravating systemic inflammation and metabolic imbalance (Pearce et al., 2013) ^[63]. Chronic exposure to heat stress can ultimately lead to severe metabolic disorders such as hepatic lipidosis and ketosis (Chaidanya et al., 2017) ^[18].

Overall, the physiological response to heat stress represents a complex interplay of endocrine, metabolic, and cellular adaptations aimed at maintaining survival under adverse environmental conditions. However, these compensatory mechanisms occur at the expense of productive efficiency, resulting in reduced milk yield, impaired reproduction, and compromised health in dairy cattle.

5. Effect of heat stress on health and immune response

Exposure of dairy cattle to heat stress induces profound alterations in immune competence and overall health, leading to increased susceptibility to infectious and metabolic disorders. One of the primary consequences is immunosuppression, characterized by reduced neutrophil phagocytic activity and diminished lymphocyte proliferation, thereby impairing the animal's ability to mount an effective immune response (Tejaswi et al., 2020) ^[85]. Heat stress also affects specific immune cell populations, including reductions in WC1+ $\gamma\delta$ T cells in Jersey cattle and CD21+MHCII+ B cells in Holstein cows, indicating breed-specific immunological vulnerabilities. In indigenous breeds such as Sahiwal, decreased phagocytic activity accompanied by elevated cortisol levels further reflects compromised immune function (Alhussien and Dang, 2018) ^[2].

The mammary gland is particularly affected under heat stress conditions. Impaired synthesis of key immunoglobulins (IgA, IgM, and IgG) and altered cytokine production weaken local immune defenses, while dysfunctional neutrophil activity reduces the efficiency of bacterial clearance, increasing the risk of intramammary infections (Alhussien and Dang, 2018) ^[2]. Concurrently, elevated levels of Reactive Oxygen Species (ROS) contribute to oxidative damage, particularly at the mitochondrial level, which not only disrupts cellular integrity but also reduces milk protein synthesis and predisposes animals to mastitis (Giannone et al., 2023) ^[31].

Heat stress also induces significant hematological changes. A decline in red blood cell counts, coupled with an increase in white blood cells, reflects physiological stress and inflammatory responses (Das et al., 2016) ^[28]. Elevated cortisol levels further impair immune function by reducing L-selectin expression, thereby limiting neutrophil migration to sites of infection (Giannone et al., 2023) ^[31]. Although Heat Shock Proteins (HSPs) are upregulated as a protective response and may enhance cellular resilience, the concurrent decline in circulating immunoglobulins and persistent elevation of stress hormones disrupt overall immune balance (Tejaswi et al., 2020) ^[85].

Chronic heat stress manifests in broader health complications, including increased incidence of lameness, hepatic dysfunction, ketosis, and other metabolic disorders (Das et al., 2016) ^[28]. Alterations in rumen function further exacerbate metabolic instability, increasing vulnerability to digestive

disorders. Periparturient cows are particularly at risk, as heat stress combined with conditions such as hypocalcemia further compromises thermoregulation and health status.

Importantly, the effects of heat stress extend beyond the individual animal to subsequent generations. Offspring born to heat-stressed dams exhibit impaired immune function, including reduced expression of key immune markers, altered hematological profiles, and decreased transfer of passive immunity (IgG) (Tejaswi et al., 2020) ^[85]. These calves often display reduced birth weights and increased susceptibility to diseases such as pneumonia and diarrhea, indicating long-term developmental consequences (Tejaswi et al., 2020) ^[85]. Collectively, these findings highlight the extensive and multifactorial impact of heat stress on immune function, health, and intergenerational performance in dairy cattle.

6. Heat stress mitigation strategies

Effective mitigation of heat stress in dairy cattle requires an integrated approach encompassing housing design, environmental modification, and nutritional management to minimize thermal load and sustain productivity (Zeng et al., 2022) ^[97].

6.1 Livestock housing and space management

Provision of adequate shade is a fundamental strategy to reduce the impact of solar radiation, thereby lowering surface body temperature and respiration rate in heat-stressed cattle (West, 2003) ^[89]. Shaded environments enhance animal comfort by encouraging feed intake and resting behavior during periods of high ambient temperature, ultimately reducing production losses (Polsky and von Keyserlingk, 2017) ^[67].

6.2 Thermal management and ventilation

Structural modifications such as reflective roofing materials, optimal farm orientation, and shaded sidewalls are effective in limiting solar heat gain within housing facilities. These measures facilitate heat dissipation through conduction and convection, thereby improving the microclimate within the barn (West, 2003) ^[89]. Adequate ventilation, whether natural or mechanical, plays a critical role in enhancing air movement around the animal, promoting convective heat loss and reducing heat load. Although ventilation alone may be insufficient under hot and humid conditions, even modest increases in air velocity can significantly reduce physiological stress indicators such as respiration rate and rectal temperature (Polsky and von Keyserlingk, 2017; Giannone et al., 2023) ^[31, 67].

6.3 Cooling systems (fans and evaporative cooling)

The use of cooling fans is an effective method to enhance convective heat loss and improve animal comfort and feed intake under heat stress conditions (West, 2003) ^[89]. When combined with evaporative cooling techniques such as sprinklers or misters, the efficiency of heat dissipation is markedly improved. These systems facilitate evaporative heat loss, resulting in reductions in body temperature and respiration rate. Fan-sprinkler combinations are particularly effective as short-term interventions for rapidly alleviating acute heat load, especially in lactating dairy cows (Polsky and von Keyserlingk, 2017; Tabler, 2025) ^[67].

6.4 Nutritional strategies

Dietary management is a critical component in mitigating the adverse effects of heat stress. Adjustments in feeding

strategies should aim to maintain energy intake while minimizing metabolic heat production (Table 2). This can be achieved by strategically reducing dietary fiber levels, ensuring optimal rumen function, and increasing the energy density of the diet. The inclusion of rumen undegradable protein (RUP) enhances amino acid availability for milk

synthesis while avoiding excessive ammonia production associated with highly degradable protein sources (Wheelock et al., 2010) [90]. Supplementation with dietary fats provides an additional energy source with lower heat increment, thereby supporting production under heat stress conditions (Wang et al., 2025) [89].

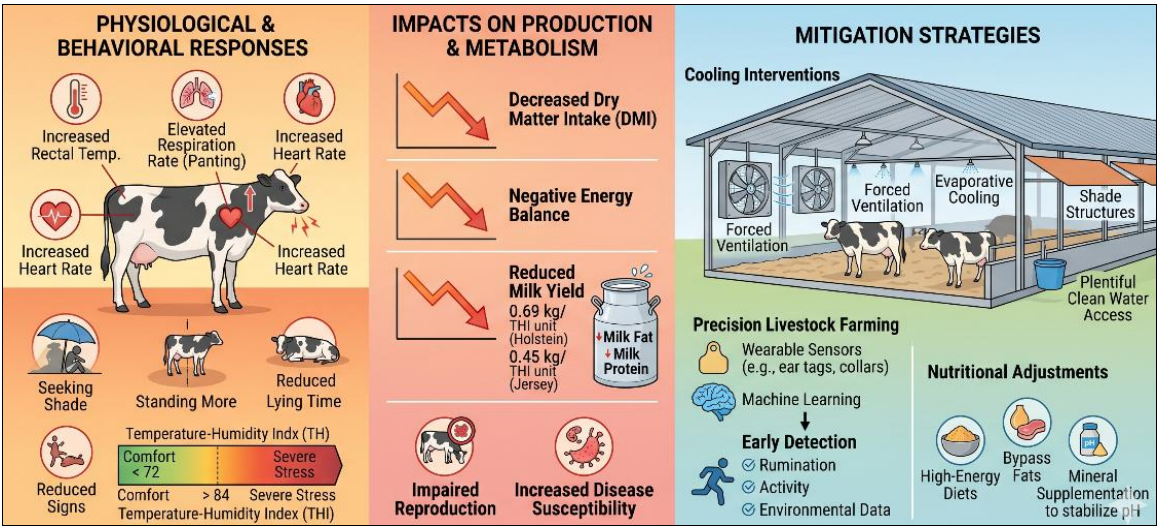


Fig 1: Comprehensive Overview of Heat Stress Responses and Mitigation Strategies

Maintaining electrolyte balance is equally important, particularly through supplementation of potassium, sodium, and magnesium, along with optimizing Dietary Cation-Anion Difference (DCAD) levels, typically in the range of +20 to +30 meq/100 g dry matter, to support acid-base balance and improve feed intake and milk production (West, 2003; Baumgard and Rhoads, 2013) [70, 89]. Additionally, the provision of cool drinking water and electrolyte solutions plays a vital role in alleviating heat stress by supporting hydration and thermoregulation (Wang, 2025) [89]. Heat stress also leads to significant losses of electrolytes, including potassium, sodium, and bicarbonate, through increased sweating and urinary excretion. Supplementation of these minerals, along with micronutrients such as selenium and chromium, plays a crucial role in maintaining acid-base balance, thermoregulation, and immune function (Reddy et al., 2023) [69]. Adjustment of dietary cation-anion difference

(DCAD) has also been demonstrated to improve systemic acid-base status and enhance milk fat synthesis (Bertens et al., 2024) [10]. Additionally, feed additives such as yeast cultures, plant-derived bioactive compounds, organic acids, and antioxidants (e.g., vitamins E and niacin) contribute to improved rumen stability, reduced oxidative stress, and enhanced immune responses (Wang et al., 2025) [89]. Continuous access to clean and cool drinking water remains essential for maintaining hydration, supporting thermoregulation, and sustaining feed intake under heat stress conditions (Reddy et al., 2023) [69]. Overall, the integration of environmental, managerial, and nutritional interventions is essential to effectively mitigate heat stress and sustain productivity and welfare in dairy cattle under challenging climatic conditions.

Table 2: Feed additives, bioactive compounds, and essential oils for heat stress mitigation in dairy cattle

Category	Additive	Dose	Key Effects	References
Antioxidants	Vitamin E + Selenium	Se: 0.3 mg/kg DM; Vit E: 80 IU/kg DM	↑ Milk yield; ↓ SCC & mastitis; ↑ immunity	Chen et al., 2023 [21]
	Vitamin C	50-100 mg/kg BW/day	↑ Antioxidant status; ↓ SCC	Padilla et al., 2006 [61]
	Zn, Cu, Mn	As per requirement	↓ Oxidative stress; ↑ immune function	Chen et al., 2023 [21]
Electrolytes	Electrolyte mix	50-100 g/day	↑ DMI; maintains electrolyte balance	West, 2003 [89]
	Betaine	15-30 g/day	↑ Milk yield; improves heat tolerance	Malik et al., 2024 [54]
Energy Source	Rumen-Protected Fat	150-200 g/day	↑ Milk yield; improves energy balance	Rhoads et al., 2013 [70]
Probiotics	Yeast + LAB	5-10 g/day	↑ Digestibility; ↑ DMI; ↓ mastitis	Habimana et al., 2023 [34]
Herbals	Turmeric	5-15 g/day	↓ Oxidative stress; ↑ thermotolerance	Grewal et al., 2022 [32]
	Tulsi + Neem	10-50 g/day	↓ Stress; ↑ immunity	Jamshidi & Cohen, 2017 [38]
	Ginger	5-15 g/day	↑ Feed intake; anti-inflammatory	Jamshidi & Cohen, 2017 [38]
	Black cumin + EO	10-30 g/day	↑ Antioxidant status	Wickramasinghe et al., 2023 [92]

6.5 Cooling strategies and environmental management

Environmental modification is a critical component of heat stress mitigation. The combined use of fans and sprinklers is widely recognized as an effective approach to enhance evaporative cooling and reduce thermal load. Intermittent water application followed by adequate drying periods

optimizes evaporative efficiency while preventing excessive moisture accumulation. The use of high-capacity fans with adjustable airflow further enhances convective heat loss and improves animal comfort (Schutz et al., 2011) [75]. Housing design plays a significant role in thermal regulation. Open-sided structures with sufficient height promote natural

airflow and reduce heat accumulation within the facility. In regions characterized by high humidity, such as tropical climates, sprinkler systems are generally more effective than fine misting systems, as larger water droplets facilitate direct cooling of the animal's body surface. However, proper management is essential to avoid issues such as wet bedding and hygiene concerns (Kadzere et al., 2002) ^[40]. In contrast, high-pressure fogging systems are more suitable for dry environments, where evaporative cooling efficiency is higher. Integration of multiple cooling technologies is often necessary to effectively manage heat stress under diverse environmental conditions and maintain optimal production levels.

6.6 Long-term mitigation strategies: genetic approaches

In regions with persistently high temperature and humidity, long-term adaptation strategies are essential to sustain dairy productivity. Genetic improvement through crossbreeding offers a practical approach to enhance heat tolerance. Incorporation of thermotolerant traits from indigenous breeds, particularly *Bos indicus*, into high-producing *Bos taurus* populations can improve both reproductive performance and resilience to heat stress. For example, the introduction of heat-tolerant genetics into Holstein populations has been shown to enhance fertility and maintain milk production under thermal stress conditions (Kadzere et al., 2002) ^[40].

Advancements in genomic technologies have further expanded opportunities for selective breeding. Tools such as whole-genome sequencing and single nucleotide polymorphism (SNP) arrays enable the identification of genetic markers associated with thermotolerance, facilitating the development of climate-resilient dairy cattle (Kadzere et al., 2002) ^[40]. Successful breeding programs, such as the development of the Girolando breed in tropical environments, demonstrate the potential of combining productivity with adaptability (Chen, 2023) ^[21]. However, a critical balance must be maintained, as increased heat tolerance is often associated with reduced production potential under non-stress conditions (Bohmanova et al., 2008) ^[12]. Therefore, future breeding strategies should aim to optimize both productivity and environmental resilience to ensure sustainable dairy production under changing climatic conditions.

7. Emerging technologies for heat stress monitoring and management

The adoption of precision livestock technologies is gradually increasing in dairy production systems, including those in developing regions such as Bangladesh. Sensor-based monitoring tools—such as wearable temperature tags, rumen boluses, and infrared thermography—enable continuous assessment of both environmental conditions and animal physiological status. These technologies facilitate early detection of heat stress by tracking indicators such as body temperature, rumen activity, and behavioral changes. Integration of these devices with artificial intelligence (AI)-driven algorithms further enhances decision-making by providing real-time, condition-specific management recommendations to mitigate thermal stress and improve overall herd performance (Malik, 2023) ^[54].

7.1 Integrated approach: environmental, nutritional and genetic strategies

Effective mitigation of heat stress requires a holistic approach that combines environmental modification, nutritional optimization, and genetic improvement. Environmental interventions, including provision of shade, enhanced

ventilation, and evaporative cooling systems, remain the most immediate and effective strategies to reduce thermal load (Atrian and Shahryar, 2012) ^[3]. The integration of cross-ventilation with evaporative cooling has been shown to improve milk yield, reproductive efficiency, and feed utilization (Kadokawa et al., 2012). Ensuring continuous access to clean, cool drinking water is equally critical, as water intake increases substantially with rising ambient temperatures.

Nutritional strategies complement environmental management by supporting metabolic adaptation under heat stress. High-energy diets, achieved through increased concentrate feeding and fat supplementation, help compensate for reduced feed intake while minimizing heat increment (Atrian and Shahryar, 2012) ^[3]. Protein nutrition also plays a crucial role, with diets containing higher levels of rumen-undegradable protein supporting improved milk production under thermal stress. Supplementation with antioxidants such as vitamins C, E, and A, along with trace minerals like zinc, helps mitigate oxidative stress and maintain immune function (Das et al., 2016) ^[28]. Additives such as yeast cultures and niacin further enhance rumen fermentation and metabolic efficiency during heat stress conditions (Panda et al., 2017). Additionally, replenishment of electrolytes, particularly sodium and potassium, is essential to counteract losses through sweating and maintain physiological balance (Kadzere et al., 2002) ^[40]. Increasing feeding frequency may also reduce heat load associated with digestion and improve nutrient utilization.

Genetic strategies provide a long-term solution by enhancing inherent thermotolerance in dairy cattle. Animals with phenotypic traits such as lighter coat color and shorter hair exhibit improved heat tolerance (Bernabucci et al., 2010) ^[9]. At the molecular level, genes associated with heat shock proteins, particularly HSP70, play a crucial role in cellular protection against thermal stress. Indigenous breeds such as Sahiwal and Tharparkar, which exhibit higher expression of heat shock proteins, demonstrate superior adaptability to hot environments. Selective breeding and genomic approaches targeting these traits offer promising avenues for developing climate-resilient dairy populations.

8. Challenges in heat stress mitigation

Heat stress poses a significant and growing challenge to dairy production systems in developing countries, particularly in regions characterized by high temperature and humidity. Prolonged exposure to such conditions leads to reduced feed intake, decreased milk production, and increased incidence of health disorders. In Bangladesh, where dairy farming is predominantly practiced by smallholder farmers, several constraints limit the effective implementation of heat stress mitigation strategies (Collier, 2006) ^[23].

One of the primary challenges is the lack of awareness and technical knowledge among farmers regarding the identification and management of heat stress. Many producers fail to recognize early signs of thermal stress or lack access to appropriate advisory services. Economic limitations further restrict the adoption of advanced cooling technologies, such as tunnel ventilation and automated climate control systems, which require substantial capital investment.

Climatic factors also exacerbate the problem. High relative humidity in tropical and subtropical regions reduces the efficiency of evaporative cooling mechanisms, such as sweating and misting systems, thereby increasing the overall heat load on animals. Infrastructural constraints, including unreliable electricity supply, limit the use of mechanical

ventilation and cooling systems. Although renewable energy sources such as solar power offer potential alternatives, their initial installation costs remain prohibitive for small-scale farmers.

Additionally, traditional housing designs with inadequate ventilation, low roof height, and poor orientation contribute to heat accumulation within animal shelters. Nutritional management during heat stress also presents economic challenges, as the provision of high-quality, nutrient-dense feed required to offset reduced intake increases overall production costs. Failure to address these constraints often results in negative energy balance, reduced productivity, and compromised animal welfare.

Collectively, these challenges highlight the need for cost-effective, scalable, and region-specific strategies that integrate technological innovation, farmer education, and policy support to effectively mitigate heat stress in dairy production systems.

9. Conclusion

Heat stress is a major constraint to sustainable dairy production, significantly affecting physiological function, metabolism, reproduction, immunity, and overall productivity. The disruption of thermal balance induces complex adaptive responses that, while essential for survival, result in reduced feed intake, milk yield, and health status. At the cellular level, oxidative stress and endocrine disturbances further intensify production losses and disease susceptibility.

The severity of heat stress is governed by environmental conditions and animal-related factors such as breed, lactation stage, and production level. Prolonged exposure leads to cumulative and persistent declines in performance, with potential long-term effects on offspring. These challenges are particularly critical in tropical and subtropical regions, where climatic stress and resource limitations are pronounced.

Mitigation requires an integrated approach combining environmental management, nutritional strategies, and genetic improvement. Emerging precision technologies offer opportunities for early detection and targeted interventions, although their adoption remains limited in smallholder systems due to economic and infrastructural constraints.

Future efforts should focus on developing cost-effective, region-specific solutions that enhance resilience while maintaining productivity. Strengthening farmer awareness, improving access to technology, and advancing genetic selection for thermotolerance are essential to ensure sustainable dairy production under changing climatic conditions.

Conflict of interest statement

The authors declare that there are no conflicts of interest regarding the publication of this review. The research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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