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HEAT STRESS IN CATTLE: IMPACTS ON PHYSIOLOGY, REPRODUCTIVE PERFORMANCE, AND MITIGATION THROUGH GENETIC AND ENVIRONMENTAL STRATEGIES (A REVIEW)

A. Mohammed[1], H.A. Modu-Kagu[2], A.O. Abdulraheem[2], M.M. Shattima[1], M. Kaganami[1], J. Aliyu[2], A.O. Raji[2] and K.N. Alade[2]

[1]Department of Animal Science, Borno State University, 1122, Maiduguri, Borno State

[2]Department of Animal Science, Faculty of Agriculture, University of Maiduguri, P.M.B. 1069, Maiduguri, Borno State, Nigeria

Correspondence: banayeyya@yahoo.com 08033413930

ABSTRACT: Heat stress is an increasingly critical challenge in cattle production, exacerbated by global climate change and a rising ambient temperature. This review explores the multifaceted impacts of heat stress on cattle, highlighting its effects on thermoregulation, metabolism, reproductive efficiency, milk production, growth performance, and overall animal welfare. Physiological and cellular mechanisms involved in heat stress response, including behavioral adaptations and the role of heat shock proteins, are also discussed in detail. The review also examined current mitigation strategies, such as environmental modifications, nutritional management, hormonal interventions, and assisted reproductive technologies. Special emphasis is placed on genetic strategies for improving thermotolerance, including the use of heat-adapted breeds, genomic selection, and identification of key molecular markers. While considerable progress has been made, challenges such as genetic antagonisms and limited resources in arid zones continue to hinder large-scale implementation. Integrating genetic selection with sustainable management practices offers a viable path toward improving cattle resilience and productivity under heat stress conditions.

Keywords: heat stress, thermoregulation, milk production, genetic selection, climate change, livestock management

INTRODUCTION

Climate change and global warming have led to a significant increase in the frequency and intensity of heatwaves across both tropical and temperate regions (IPCC, 2023). According to the Intergovernmental Panel on Climate Change (IPCC), human-induced climate change has increased the frequency and intensity of heatwaves since the 1950s, with additional warming projected to further amplify these extremes. The IPCC's Sixth Assessment Report also highlights that every additional increment of global warming causes discernible increases in the intensity and frequency of temperature extremes, including heatwaves (Russo *et al*., 2017; IPCC, 2023). These extreme weather events pose serious challenges to livestock production systems, especially in cattle, due to their sensitivity to elevated ambient temperatures and humidity. High environmental temperatures, when combined with solar radiation and poor ventilation, lead to heat stress, a physiological condition in which the animal fails to adequately dissipate body heat to maintain thermal balance (Mader, 2014; Perkins-Kirkpatrick & Lewis, 2020).

Ruminants, particularly high-yielding dairy cattle, are highly susceptible to heat stress due to their elevated metabolic heat production from rumen fermentation and the demands of lactation. This increased metabolic activity generates substantial internal heat, making it challenging for these animals to dissipate excess heat, especially under high ambient temperatures (Dahl & Holub, 2022; Nutrinews, 2024). The resulting physiological strain not only reduces feed intake and milk yield but also negatively impacts reproductive performance and immune function, culminating in substantial economic losses and compromising animal welfare (West, 1994; Collier *et al*., 2006;

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North *et al*., 2023). The situation is particularly alarming in developing countries where mixed farming systems dominate, and livestock are essential for food security, income, and livelihood. Climate projections indicate that the incidence and severity of heat stress will continue to rise, especially in tropical and subtropical regions (IPCC, 2022). As a result, addressing heat stress has become an urgent priority for sustainable livestock development (Morton, 2007; Thornton *et al*., 2009).

This review synthesized current knowledge on the causes and consequences of heat stress in cattle, outlines the physiological, cellular, and reproductive impacts, and explored various management and genetic strategies to mitigate its effects. A special focus is placed on the role of genetic selection and adaptation as long-term solutions to enhance thermotolerance in cattle under changing climatic conditions.

Understanding Heat Stress in Cattle

Definition and Mechanisms

Heat stress occurs when the net heat load on an animal exceeds its capacity to dissipate heat, leading to elevated body temperature and physiological strain. This condition can result from high ambient temperature, humidity, solar radiation, and low air movement, collectively referred to as the Temperature-Humidity Index (THI) (Zimbelman *et al.,* 2020). Ruminants gain heat from solar radiation, high ambient temperature, and humidity, and also generate additional metabolic heat through rumen fermentation (Mader, 2014). Cattle are particularly susceptible due to their high basal metabolic rate and limited ability to dissipate heat through sweating, unlike other species (West, 1994; Islam *et al*., 2021).

Mechanism and Causes of Heat Stress

Heat stress is a critical environmental challenge affecting cattle worldwide, especially in tropical and subtropical climates. It compromises animal welfare, productivity, reproductive performance, and health, resulting in substantial economic losses for the livestock industry. The increasing frequency and intensity of heatwaves due to climate change have amplified the urgency to understand the mechanisms and causes of heat stress in cattle (Polsky & von Keyserlingk, 2017; Sejian *et al*., 2022).

Ambient temperature and humidity are environmental conditions that collectively impact heat stress, and they are often combined into one metric called the temperature humidity index (THI). The THI has been shown to be a reliable indicator of heat stress in cattle (Dikmen and Hansen 2009). Animals can often endure higher temperatures if humidity is low, and the risk for heat stress increases dramatically as humidity increases, even at lower ambient temperatures. In addition to these daytime conditions, night time conditions (minimum wind speed, minimum solar radiation, and minimum THI) also impact heat stress in cattle, because cattle can often dissipate significant heat during the night because of low temperatures as observed by Mader *et al*. (2006) (Table 1**)** and Collier *et al*. (2006) (Figure 1).

Table 1. Cattle Comfort Advisor Categories.

Cattle Comfort Categories	Comprehensive Climate Index	Impacts	Cattle Comfort Index (℃)	Cattle Comfort Index (℉)
Heat Danger	Hot conditions: Extreme danger	Animal deaths may exceed 5%	<40	<105
Heat Caution	Hot conditions: Moderate to Severe	Decreased production, 20% or more Reduced conception, as low as 0%	30 to 40	85 to 105
Comfortable	Mild conditions		-10 to 30	15 to 85
Cold Caution	Cold conditions: Moderate to Severe	18-36% increase in dry matter intake	-10 to -30	15 to -20
Cold Danger	Cold conditions:	Extreme danger	<-30	<-20

Source: Mader *et al*. (2010).

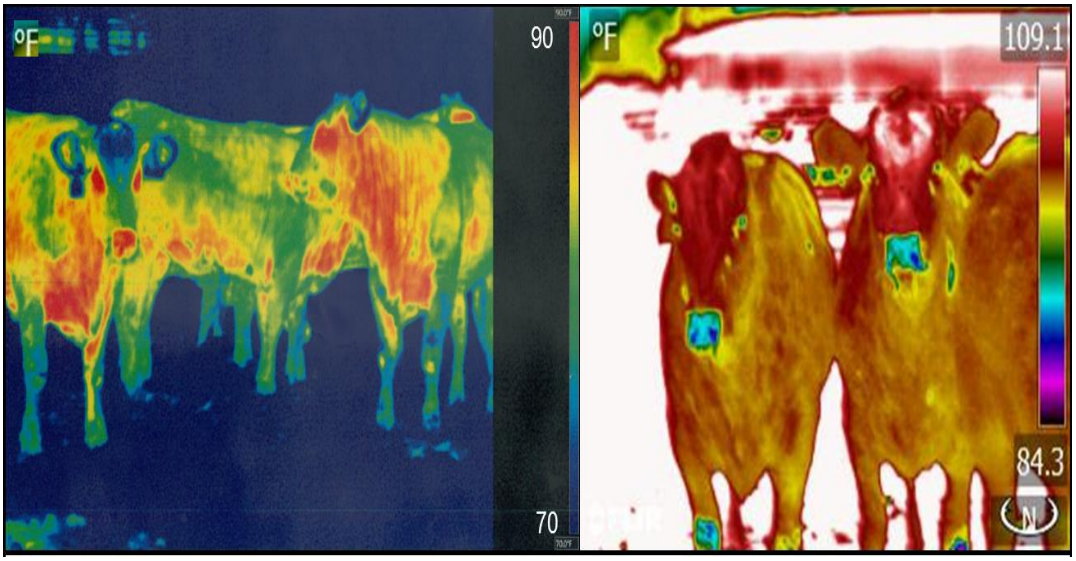

Figure 1: Thermal images showing cattle that are warmer than the surrounding environment (left), so the environment serves as a heat sink for cooling the cattle contrasted with the cattle that are in a hot environment (right) where it will be very difficult for them to dissipate heat and maintain their body temperatures. Temperature scales are provided on the right sides of each image.

Source: Collier *et al*. (2006)

Characteristics of individual animals can also position them at higher risk for heat stress. Hide colour is a well-known risk factor because dark hair has lower reflectanct values, dark skin absorbs a greater proportion of solar radiation (da Silva *et al*. 2003). Predictably, animals with black hides spend significantly more time in the shade (89%) than white (55%) (Gebremedhin *et al*., 2011). Dark-hided cattle are 25% more stressed at temperatures above 25 degrees Celsius when compared to light-hided cattle (Brown-Brandl *et al*. 2006) and exhibit 5.7x higher mortality risk in the feedlot (Hungerford *et al*., 2000). A study by Brown-Brandl *et al*. (2006) also identified other risk factors for heat stress aside from hide colour, including history of respiratory pneumonia, level of fatness, and temperament. These authors also established that excitable animals were 3.2% more stressed than their calm counterparts. Treatment history for respiratory pneumonia increased heat stress by 10.5% (Gebremedhin *et al*., 2011).

There are also internal physiological issues that contribute to heat stress. For example, greater amounts of fat in heavier cattle cause them to suffer from heat stress more and, similarly, lactating cattle have more internal heat to dissipate than non-lactating animals. Some forage plants such as tall fescue and perennial ryegrass can be endophyte infected, producing alkaloids that raise deep body temperature in cattle. 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 (Collier *et al*., 2008). Metabolism and productivity run parallel and therefore, high-producing cows are affected more than low-producing cows as a result of the TNZ downward shift (Coppock *et al*., 2002).

Environmental and Climatic Causes of Heat Stress

Ambient temperature and relative humidity are the primary drivers of heat stress. When THI exceeds critical thresholds (typically THI > 72), cattle begin to exhibit physiological stress responses (Ma *et al*., 2019). Additionally, solar radiation increases surface heat load, and poor ventilation in barns exacerbates the accumulation of heat (Lees *et al*., 2020). Climate models predict a rise in global temperatures, particularly in tropical and subtropical zones, where many cattle populations are located (Rojas-Downing *et al*., 2017).

Measurement of Heat Stress

The Temperature-Humidity Index (THI) is a widely used indicator for assessing heat stress levels in cattle (Dikmen and Hansen, 2009; Islam *et al*., 2021). THI integrates ambient temperature and relative humidity to estimate the thermal burden on livestock. Decision support tools, such as the Cattle Comfort Advisor, incorporate metrics like the Comprehensive Climate Index (CCI) to provide more precise assessments of physiological heat load (Mader *et al*., 2010). These indices help guide management decisions and intervention timing.

Temperature-Humidity Index (THI)

One of the most commonly used indices to estimate heat stress in animals. Formula (for Celsius): $THI = T - (0.55 - 0.0055 \times RH) \times (T - 14.5)$. Where: T = Dry bulb temperature (°C), RH = Relative humidity (%). Alternate Formula (for Fahrenheit): $THI = (1.8 \times T + 32) - (0.55 - 0.0055 \times RH) \times (1.8 \times T - 26)$

Heat Load Index (HLI)

Used for feedlot cattle or outdoor livestock. Formula (when black globe temperature > 25°C): $HLI = 8.62 + (0.38 \times RH) + (1.55 \times BGT) + (0.5 \times T) - (0.0055 \times RH \times T)$. Where: BGT = Black globe temperature (°C), T = Ambient air temperature (°C), RH = Relative humidity (%).

Equivalent Temperature Index for Cattle (ETIC)

Combines temperature and wind speed effects. Formula: $ETIC = T - (0.31 - 0.31 \times WS) \times (T - 14.4)$. Where: T = Dry bulb temperature (°C), WS = Wind speed (m/s)

Benezra's Thermal Comfort Index (BTCI)

Evaluates the thermoregulatory capacity of animals using physiological responses. Formula: $BTCI = (RT/38.33) + (RR/23)$. Where: RT = Rectal temperature (°C), RR = Respiratory rate (breaths/min). Lower values (<2.0) indicate better heat tolerance.

Iberia Heat Tolerance Coefficient (HTC)

Used to evaluate breed adaptability under heat stress. Formula: $HTC = 100 - 10 \times (RT - 38.3)$ HTC = 100 - 10 \times (RT - 38.3). Where: RT = Rectal temperature (°C). A higher HTC indicates better heat tolerance.

Environmental Stress Index (ESI)

Combines multiple environmental parameters. Formula: $ESI = 0.63 \times T + 0.37 \times BGT + RH \times 0.0027$. Where: T = Air temperature (°C), BGT = Black globe temperature (°C), RH = Relative humidity (%).

Respiratory Rate Index (RRI)

Assesses animal response to heat stress based on breathing. Formula: $RRI = RR/RR\ normal$. Where: RR = Observed respiratory rate, RR normal = Normal respiratory rate for the species/breed

Thermal Circulation Index (TCI)

Measures the ability of the cardiovascular system to dissipate heat. Formula: $TCI = HR \times RR$. Where: HR = Heart rate (beats/min), RR = Respiratory rate (breaths/min). Higher TCI indicates more physiological strain (Yang, *et al*., 2024).

Physiological and Behavioral Mechanisms in Responses to Heat Stress

Heat stress leads to several behavioural and physiological changes in cattle aimed at maintaining homeostasis. Cattle commonly exhibit increased respiration rates, open-mouth breathing, excessive salivation, and elevated time spent standing or seeking shade to facilitate heat dissipation (Silpa *et al.,* 2023; Pomarico *et al*., 2023). Panting and drooling are typical behavioural responses indicating elevated core body temperatures (Poudel *et al.,* 2023). Physiologically, heat stress leads to reduced feed intake and altered drinking behaviour, contributing to a negative energy balance and compromised productivity (Tao & Dahl, 2020; Silpa *et al*., 2023). These changes are often accompanied by increased heart rate and core temperature, along with hormonal and metabolic shifts that further impair growth, reproduction, and milk yield (da Silva *et al*., 2023; Collier *et al*., 2021). Heat stress triggers a cascade of physiological and behavioral adaptations in cattle aimed at maintaining thermal equilibrium. More recent studies using accelerometer-based ear tags and precision livestock tools have shown that cattle under thermal stress significantly increase their standing time, panting, and shade-seeking behavior (Islam *et al*., 2021; Pomarico *et al.,* 2023). These behaviors, though adaptive, reduce time spent lying and ruminating, which are essential for digestion and productivity.

Recent findings also indicate that rumination time decreases by over 30% during severe heat events, accompanied by increased body surface temperatures and elevated respiration rates (Silpa *et al.,* 2023). These indicators are now being integrated into automated decision tools for early heat stress detection.
Cattle respond to heat stress through a combination of behavioural, physiological, and cellular mechanisms.

i. **Behavioural Responses**: These include increased water intake, decreased feed intake, seeking shade, and reduced movement (Abdollahi *et al*., 2019).
ii. **Physiological Responses**: Heat stress induces panting, increased respiration rate, vasodilation, and elevated rectal temperature. These changes aim to dissipate excess heat but also reduce feed efficiency and milk yield in dairy cattle (Collier *et al.,* 2019).
iii. **Hormonal and Metabolic Adjustments**: Elevated cortisol and reduced insulin levels are common. These hormonal shifts alter energy metabolism and contribute to reduced growth and fertility (Belhadj Slimen *et al*., 2019).

General Effects

Heat stress leads to several behavioral and physiological changes in cattle aimed at maintaining homeostasis. Animals exhibit increased respiration rates, excessive salivation, open-mouth breathing, and increased time spent standing or seeking shade (West, 2003). Panting and drooling are common behavioral responses that reflect elevated body temperatures. Physiologically, feed and water intake typically decline, contributing to negative energy balance and reduced productivity (Silanikove, 1994).

Cellular and Molecular Responses Mechanisms

Heat stress is a significant challenge in livestock production, adversely affecting animal health, productivity, and welfare. At the cellular level, animals activate a range of responses to counteract the detrimental effects of elevated temperatures (Yang, *et al*., 2024). At the cellular level, heat stress triggers the expression of heat shock proteins (HSPs), especially HSP70, which protect cellular structures from damage due to protein denaturation (Rashamol *et al*., 2021). These proteins help maintain protein integrity and prevent aggregation or misfolding during thermal stress (Lindquist, 1993; Jaattela, 1999; Islam *et al*., 2021). Heat also induces oxidative stress, increasing reactive oxygen species (ROS) that cause lipid peroxidation, DNA damage, and apoptosis (Archana *et al*., 2020). Additionally, heat stress affects immune function by altering cytokine profiles and reducing leukocyte activity, thereby compromising the animal's resistance to diseases (Creagh *et al*., 2000; Sejian *et al.,* 2022).

Heat Shock Proteins (HSPs)

HSPs, particularly HSP70 and HSP90, are among the first lines of defence against heat stress. They function as molecular chaperones, assisting in protein folding and preventing aggregation of denatured proteins. Recent studies have shown that heat-tolerant dairy cows exhibit higher expression levels of HSP70, correlating with improved thermotolerance and reduced physiological stress indicators (Yang, *et al*., 2024).

Oxidative Stress and Antioxidant Responses

Heat stress leads to the overproduction of reactive oxygen species (ROS), resulting in oxidative damage to cellular components. To mitigate this, animals enhance their antioxidant defence mechanisms. For instance, proteomic analyses in Caracu beef cattle have identified upregulation of antioxidant enzymes like catalase (CAT) and glutathione peroxidase (GPx) in heat-tolerant individuals (Silva & Lima, 2024).

Inflammatory and Immune Responses

Elevated temperatures can trigger inflammatory responses, characterized by increased levels of pro-inflammatory cytokines. In poultry, heat stress combined with lipopolysaccharide exposure has been shown to alter gene expression in immune cells, indicating a synergistic effect on the immune response. In dairy cows, heat stress has been associated with elevated cortisol levels and altered immune cell function, particularly in heat-sensitive individuals Zhang *et al.,* 2023; Yang, *et al*., 2024).

Mitochondrial Dysfunction

Mitochondria are crucial for energy production, and their function is compromised under heat stress. Heat-induced mitochondrial dysfunction leads to decreased ATP production and increased ROS generation. Studies have highlighted the role of mitochondrial bioenergetics in dairy cattle, emphasizing the need for further research into mitochondrial adaptations to heat stress Smith & Johnson 2024).

Endoplasmic Reticulum (ER) Stress and Unfolded Protein Response (UPR)

Heat stress disrupts protein folding in the ER, leading to ER stress and activation of the UPR. This response aims to restore ER homeostasis by halting protein translation, degrading misfolded proteins, and upregulating molecular chaperones. While specific studies in livestock are limited, the UPR is recognized as a critical cellular response to heat-induced protein misfolding (Silva & Lima, 2024).

Apoptosis and Autophagy

Severe or prolonged heat stress can lead to programmed cell death (apoptosis) or autophagy. Apoptosis eliminates damaged cells, while autophagy recycles cellular components. In dairy cows, heat-sensitive individuals have shown increased markers of apoptosis under heat stress conditions, suggesting a link between heat sensitivity and cell death pathways (Yang, *et al*., 2024).

Genetic and Breed Differences

There is considerable genetic variation in heat tolerance among cattle breeds. *Bos indicus* cattle, such as the Brahman, are more heat tolerant due to physiological adaptations like lighter coat colour, increased sweating rates, and lower metabolic heat production, compared to *Bos taurus* breeds like Holstein (da Silva *et al*., 2020). Genomic studies have identified candidate genes (e.g., ATP1A1, HSP70, SOD1) associated with heat tolerance, opening avenues for breeding programs to select for thermotolerant animals (Min *et al*., 2017; Dikmen *et al*., 2018).

Nutritional and Management Factors

Poor nutrition exacerbates heat stress by limiting energy and electrolyte availability. High-protein diets increase heat production through elevated metabolic activity. In contrast, strategic feeding (e.g., high-energy, low-protein rations) and supplementation with antioxidants (e.g., selenium, vitamin E) can mitigate oxidative stress during hot periods (Tao *et al*., 2020). Management practices such as shade provision, fans, sprinkler systems, and adjusted feeding times (early morning or late evening) are practical methods to alleviate heat load in cattle (Lees *et al*., 2020).

Thermoregulatory Mechanisms

Cattle employ both sensible and latent heat loss strategies to regulate body temperature. Sensible heat loss occurs through radiation, conduction, and convection, while latent heat loss occurs through sweating and evaporative cooling via respiration (Finch, 1986; West, 2003). However, as environmental temperature and humidity increase, these cooling mechanisms become less effective, making evaporative cooling the primary method of heat dissipation (Collier *et al*., 2006; North *et al*., 2023). Variability in thermoregulatory efficiency can be influenced by animal characteristics such as coat colour, skin thickness, and sweat gland density (da Silva *et al.,* 2003; Brown-Brandl *et al*., 2006).

Reproductive Consequences of Heat Stress

Female Reproduction

Heat stress negatively impacts female reproductive function at multiple stages, from follicular development to conception and embryo viability. Elevated temperatures disrupt the hypothalamic-pituitary-gonadal (HPG) axis, leading to hormonal imbalances that impair estrous behaviour, ovulation, and luteal function (Dash *et al*., 2016). The activation of the hypothalamic-pituitary-adrenal (HPA) axis during stress stimulates cortisol secretion, which suppresses gonadotropin-releasing hormone (GnRH), luteinizing hormone (LH), and follicle-stimulating hormone (FSH) levels, thus compromising ovarian function (Roth *et al*., 2000; Hansen, 2009).

Heat stress also induces apoptosis in ovarian follicles and alters oocyte maturation, reducing the likelihood of successful fertilization (Ozawa *et al.,* 2005). Additionally, the uterine environment becomes less supportive of early embryonic development, leading to increased embryonic mortality (Al-Katanani *et al.,* 2002; Masoumi and Derensis, 2013). These factors contribute to lower conception rates, extended calving intervals, and reduced fertility in heat-stressed females (Wolfenson and Roth, 2000).

More recent studies confirm earlier findings that heat stress impairs both male and female reproductive functions. In dairy cows, follicular dynamics and luteal phase duration are shortened, while estrus intensity is diminished (Poudel *et al*., 2023). In bulls, elevated scrotal temperatures cause DNA fragmentation and reduced sperm viability, even with brief exposure (Mokhtari *et al*., 2022).

Embryo survival rates post-implantation are also significantly reduced under heat stress, leading to an increase in early embryonic loss. Embryo transfer (ET) with thermotolerant donors or cryopreserved embryos is gaining ground as a mitigation strategy (Stewart et al., 2021).

Male Reproduction

In males, spermatogenesis is highly sensitive to elevated scrotal temperatures. Testicular function requires a temperature of 4–6°C below core body temperature; heat stress impairs thermoregulation, leading to testicular degeneration, decreased semen quality, and reduced fertility (Mishra et al., 2013; Moreira and Rodrigues, 2015). Bulls exposed to high ambient temperatures exhibit lower sperm motility, reduced sperm concentration, and increased morphological abnormalities (Brito *et al*., 2004).

Prolonged heat stress compromises the structure of Sertoli and Leydig cells and induces oxidative damage to spermatozoa DNA and, further diminishing fertility (Nichi *et al.,* 2006; Nardone *et al*., 2010). Moreover, libido and sexual behaviour are often reduced due to hormonal imbalances triggered by chronic thermal stress (Chebel *et al*., 2004; Ruediger *et al.,* 2016). These impacts collectively hinder reproductive efficiency and limit the genetic progress of heat-stressed cattle populations.

Effects of Heat Stress on Livestock Productivity and Health

Milk Production

Heat stress significantly reduces milk yield and alters milk composition in dairy cattle. The decline in milk production is primarily attributed to decreased feed intake, negative energy balance, and impaired endocrine function (Spiers *et al.,* 2004). Under thermal stress, cows prioritize thermoregulation over productive functions, leading to a diversion of metabolic energy away from lactation. Studies have shown that high-producing Holstein cows can experience reductions in milk yield of up to 40% under severe heat stress conditions (West, 2003). In addition, milk fat and protein content may be negatively affected due to altered rumen function and nutrient absorption.

In dairy systems, recent meta-analyses show a loss of 1.5 to 2.5 kg of milk/cow/day for every 10-unit increase in THI above the thermal comfort threshold (Hammami *et al.,* 2022). Feed efficiency also declines, particularly in high-yielding Holstein cows. Meanwhile, beef cattle in extensive systems experience reduced average daily gain (ADG) and higher morbidity due to compromised immunity (North *et al*., 2023). Heat stress exacerbates subclinical conditions such as mastitis, acidosis, and laminitis. Gut permeability ("leaky gut") has been increasingly recognized as a central health challenge, heightening endotoxin release and systemic inflammation (López *et al*., 2021).

Growth and Feed Efficiency

Heat-stressed animals experience a substantial reduction in average daily gain (ADG) and feed conversion efficiency. Reduced voluntary feed intake and changes in metabolic rate compromise growth performance, particularly in feedlot cattle. Moreover, the efficiency of nutrient utilization declines as energy is redirected toward maintaining thermal homeostasis. Lymphocyte proliferation and protein synthesis are reduced, which impacts growth and tissue development (Sejian *et al*., 2018). The leaky gut phenomenon, caused by heat-induced intestinal damage, can also impair nutrient absorption and elevate inflammation, further limiting performance (Lyles and Calvo-Lorenzo, 2014).

Immune Function and Health

Heat stress suppresses immune competence in cattle, making them more vulnerable to disease. This occurs through several mechanisms, including elevated glucocorticoid levels that inhibit cytokine production, impaired lymphocyte proliferation, reduced phagocytic activity, and disruptions in gut microbiota composition (Kiros *et al*., 2021; Liu *et al.,* 2019; Renaudeau *et al.,* 2023). Elevated ambient temperatures compromise the intestinal barrier, increase endotoxin translocation, and provoke systemic inflammatory responses (Lyles and Calvo-Lorenzo, 2014). These effects can lead to higher incidences of mastitis, lameness, respiratory illness, and other metabolic disorders. Seasonal infertility is also exacerbated by heat stress through the disruption of normal immune and hormonal regulation, contributing to reproductive inefficiencies (Hansen, 2009). In young calves, thermal stress impairs passive immunity transfer and increases morbidity and mortality rates.

Strategies for Mitigating Heat Stress

Environmental Modifications

Environmental strategies to reduce heat stress in cattle primarily focus on altering the microclimate to minimize solar radiation and enhance heat dissipation. Providing shade, natural (trees) or artificial (roofs, shade cloths), is one of the most effective and cost-efficient methods (Buffington *et al*., 2003). Structures painted white or equipped with insulating materials can significantly reduce radiant heat load. Effective shading has been shown to lower body temperatures and improve productivity.

Cooling systems such as fans, sprinklers, and evaporative cooling techniques are widely used in confinement operations. These systems combine water misting with ventilation to reduce ambient temperatures and increase evaporative heat loss from the animal's body (Sejian *et al*., 2012). Proper placement and timing of these systems are critical to avoid excessive water accumulation, which may lead to hoof problems. Recent innovations in smart farming integrate climate sensors and automated cooling systems to adjust misting, ventilation, and shade dynamically. Use of photovoltaic-shade structures has been shown to reduce radiant heat and lower carbon footprints simultaneously (Singh *et al.,* 2022).

Nutritional Interventions

Nutritional strategies aim at reducing metabolic heat production and supporting physiological functions during heat stress. Providing high-quality, energy-dense feed helps maintain production despite reduced intake. Fat supplementation is often recommended as it increases dietary energy without elevating heat increment (Staples et al., 1998). Lowering fiber content can also minimize fermentation heat.

Supplementing trace minerals (such as but not limited to zinc, selenium, chromium) and vitamins (good examples of which are vitamin E, ascorbic acid) has shown positive effects on immune function and antioxidant capacity, helping cattle cope with oxidative stress during heat events (Alamer, 2011; Abdin and Khatoon, 2013). Additionally, electrolytes and buffers may aid in maintaining rumen pH and hydration.

Novel dietary strategies include supplementation with rumen-protected antioxidants (e.g., resveratrol, vitamin C, selenium) and electrolyte cocktails. Meta-analyses support the use of rumen-protected fat and bypass protein during heat periods to reduce fermentation heat load and maintain production (Tian *et al.,* 2021).

Hormonal and Reproductive Technologies

Hormonal therapies such as gonadotropin-releasing hormone (GnRH) and human chorionic gonadotropin (hCG) can be administered to enhance ovulation and luteal function during heat stress (Wolfenson *et al*., 2000; Samal, 2013). Protocols like Ovsynch and Presynch have been used successfully to synchronize ovulation and improve conception rates in heat-stressed animals.

Embryo transfer (ET) is another effective reproductive strategy as it bypasses the heat-sensitive early embryonic development phase. Embryos can be produced under thermoneutral conditions and transferred into recipients after the period of greatest heat stress, increasing pregnancy success rates (Stewart *et al*., 2011).

Genetic Strategies for Heat Tolerance

Breed Selection and Crossbreeding

Genetic selection for heat tolerance involves identifying and propagating animals that possess superior thermoregulatory capabilities. Indigenous breeds such as *Bos indicus* cattle are naturally more heat-tolerant than *Bos taurus* breeds due to physiological traits like lighter coat colour, higher sweating rate, larger skin surface area, and lower metabolic heat production (Hansen, 2004). These breeds maintain productivity under heat stress and are better adapted to tropical climates.

Crossbreeding strategies combine the productivity of *Bos taurus* with the heat tolerance of *Bos indicus*, resulting in hybrid vigour. For example, the use of Brahman crosses in dairy and beef operations has shown significant improvements in heat adaptability without severely compromising production traits (Burrow, 2001).

Genomic selection for thermotolerance is gaining precision with single-step GBLUP models and incorporation of genotype × environment (G×E) interactions (Cheruiyot *et al.,* 2018). Breeds such as Senepol and Sahiwal, and animals expressing the slick hair gene, are being strategically crossbred with high-producing but thermosensitive breeds (Garner *et al*., 2020).

Markers linked to thyroid hormone regulation, sweat gland density, and coat reflectance are being explored for multi-trait genomic indices (Silpa *et al*., 2023). CRISPR-Cas9 research is in early stages for introducing thermotolerance alleles into commercial breeds (Zhang *et al.,* 2023).

Genotype by Environment Interactions

Genotype by environment (G×E) interactions are crucial in understanding how genetic performance varies under different environmental conditions. Animals with high genetic merit under thermoneutral conditions may not perform optimally under heat stress. The use of reaction norm models helps evaluate genetic performance across a gradient of environmental stressors, enabling the selection of animals that exhibit greater resilience (Cheruiyot *et al*., 2018). Selection programmes that incorporate G×E interactions are better equipped to identify sires and dams that maintain reproductive and productive efficiency during heat events. Long-term breeding objectives should emphasize robustness and adaptability alongside conventional performance traits.

Genetic Markers and Genomic Tools

Advancements in molecular genetics have enabled the identification of candidate genes and markers associated with thermotolerance. Notable among these is the slick hair gene, which contributes to shorter, sleek coats and enhanced heat dissipation in tropical breeds like Senepol and Criollo (Olson *et al*., 2003). Heat shock protein genes (e.g.,

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HSP70, HSP90) are also linked to cellular protection under thermal stress. Polymorphisms in these genes have been associated with differences in heat resilience and fertility traits (Collier *et al.,* 2008).

Genomic selection tools, including genomic estimated breeding values (GEBVs), are increasingly used to integrate heat tolerance traits into selection indices. These tools allow for more accurate and early selection, particularly when combined with large-scale phenotypic and environmental data (VanRaden *et al.,* 2009).

Challenges and Limitations in Genetic Selection

Despite the potential of genetic strategies to improve heat tolerance in cattle, several challenges hinder their widespread adoption and effectiveness.

Genetic Antagonism with Productivity Traits

One of the major limitations is the potential antagonism between thermotolerance and high production traits. For instance, animals selected for enhanced heat tolerance, such as *Bos indicus* breeds, often exhibit lower milk yield or growth rates compared to their *Bos taurus* counterparts (Hansen, 2004). Balancing production and adaptability traits requires careful selection indices that account for both short-term productivity and long-term resilience.

Limited Genetic Resources and Infrastructure

In many developing countries, where heat stress is most severe, the lack of genomic infrastructure, reliable performance data, and animal recording systems restricts the implementation of advanced genetic tools (FAO, 2015). The absence of large-scale phenotypic databases and insufficient investment in animal biotechnology further compound the issue.

Complexity of Heat Tolerance Traits

Thermotolerance is a complex, polygenic trait influenced by multiple physiological and behavioural responses. This complexity makes it difficult to identify and isolate specific markers or genes responsible for heat resilience. Moreover, genotype-by-environment interactions can obscure the expression of such traits in different climates or production systems (Cheruiyot *et al*., 2018).

Institutional and Policy Barriers

Weak policy frameworks, limited funding, and lack of stakeholder collaboration pose additional barriers to the adoption of genetic solutions. Breeding programmes often prioritize productivity and market demands over environmental resilience, leading to the underrepresentation of heat-adapted indigenous breeds in national strategies (Rege *et al*., 2011).

Public Perception and Ethical Concerns

There is also public scepticism surrounding genetic modification and selective breeding, particularly in relation to animal welfare and food safety. Ethical concerns regarding biotechnology, along with varying regulatory standards across countries, can delay or prevent the deployment of genomic interventions. Addressing these limitations requires a coordinated effort among researchers, breeders, policymakers, and producers to build capacity, develop locally adapted strategies, and align breeding goals with sustainability objectives.

Future Directions and Recommendations

To build climate-resilient cattle production systems, future efforts must focus on integrating genetic strategies with holistic management practices and policy support. The following recommendations are proposed:

Integrate Breeding with Management Practices

Heat mitigation should be approached as a comprehensive strategy combining genetic improvement with environmental, nutritional, and reproductive interventions. This integrative approach enhances overall resilience and ensures consistent performance under varying climatic conditions (Sejian *et al*., 2018).

Prioritize Locally Adapted and Indigenous Breeds

Locally adapted breeds often possess inherent traits that confer resistance to heat and disease. Conservation and strategic utilization of these breeds should be prioritized through national breeding programs and genetic resource preservation initiatives (FAO, 2015). Research should focus on improving productivity while retaining adaptability.

Expand Genomic Selection and Research

Investment in genomic infrastructure, particularly in low- and middle-income countries, is essential for scaling genetic interventions. Collaborative efforts between international research institutions, governments, and private sectors can facilitate data sharing, training, and capacity building to enhance genomic selection (VanRaden *et al*., 2009).

Develop Climate-Specific Breeding Objectives

Selection indices should be revised to incorporate thermotolerance and other resilience traits, such as feed efficiency and disease resistance, alongside traditional production traits. This shift will better align breeding goals with the realities of climate change (Cheruiyot *et al*., 2018).

Foster Policy Support and Institutional Alignment

Strong institutional frameworks and enabling policies are required to promote sustainable breeding strategies. Supportive regulations, funding mechanisms, and incentives should be implemented to accelerate adoption of heat-tolerant genetics and maintain biodiversity (Rege *et al*., 2011). By addressing these future priorities. The livestock sector can enhance adaptation to climate stressors while improving productivity and sustainability.

CONCLUSIONS

Heat stress represents a growing threat to the sustainability of cattle production systems worldwide. Its adverse effects on physiological function, reproduction, productivity, and animal welfare are well documented, particularly under the intensifying influence of global climate change. As heatwaves become more frequent and severe, traditional management approaches alone may be insufficient to safeguard livestock health and performance.

This review highlights the critical need for integrated solutions that combine short-term mitigation strategies, such as environmental modifications and nutritional interventions, with long-term genetic approaches aimed at enhancing thermotolerance. The use of heat-adapted breeds, genomic tools, and targeted breeding programmes offers a promising path to resilient livestock systems.

However, successful implementation of these strategies depends on addressing significant challenges, including limited infrastructure, genetic antagonisms, and policy constraints. Future efforts must therefore prioritize capacity building, research investment, and institutional support, especially in regions most vulnerable to climate variability.
By aligning genetic improvement with climate adaptation goals, the livestock sector can achieve enhanced productivity, animal welfare, and environmental sustainability, ensuring food security in the face of an increasingly volatile climate.

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