

The impact of heat stress on global ruminant livestock production and potential adaptation and mitigation interventions

By Lee, M.R.F., Rivero, M.J. and Dunshea, F.R.

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The impact of heat stress on global ruminant livestock production and potential adaptation and mitigation interventions

Michael R. F. Lee¹, M. Jordana Rivero² and Frank R. Dunshea^{3,4}

Rising global temperatures and more frequent heat waves impose severe heat stress (HS) on ruminant livestock, threatening the sustainability of intensive and extensive production systems. This mini-review evaluates nutritional, genetic, and engineering (including nature-based) interventions designed to build livestock resilience within climate-smart food systems. HS limits feed intake, disrupts reproductive physiology and elevates disease risk. Climate modeling projections indicate that by 2050, millions of cattle, sheep, and goats will experience 10–20 additional extreme HS days annually, impacting animal welfare, and generating massive economic losses, particularly in low- and middle-income countries (LMICs). Nutritional strategies such as betaine, organic selenium, polyphenols, and chromium reduce endogenous heat production, oxidative stress, and gut permeability, thereby maintaining performance under HS. Mitigating these impacts requires an integrated deployment of targeted nutritional supplements, genomic and indigenous selection for thermotolerance, and environmental modification. This mini-review provides a critical evaluation of these multifaceted strategies, emphasizing their inherent trade-offs, economic feasibility and resources limitations.

Addresses

¹ School of Sustainable Food and Farming, Harper Adams University, Edgmond, Shropshire, TF10 8NB, UK

² Rothamsted Research, North Wyke, Okehampton, EX20 2SB, UK

³ School of Agriculture, Food and Ecosystem Sciences, The University of Melbourne, Victoria, Australia, 3010

⁴ School of Biology, Faculty of Biological Sciences, The University of Leeds, Leeds, Yorkshire, LS2 9JT, UK

Corresponding author: Dunshea, Frank R. (fdunshea@unimelb.edu.au)

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Introduction: global scale and vulnerability projections

Escalating environmental temperatures and more frequent and intense heatwaves compromise global farm sustainability by impairing animal welfare, reducing feed intake, and inducing severe production losses [1]. Utilizing an ensemble of bias-adjusted regional and global climate model projections under a range of stabilizing and high greenhouse gas emission scenarios (such as RCP4.5, RCP8.5, SSP1-2.6, and SSP5-8.5), projections show that by 2050, 6.2–13.7 million cattle in temperate Europe (11%–21.6% of current EU + UK totals) will face over 15 additional heatwave days annually, with indoor/zero-grazing confinement systems facing a two-fold higher risk (18.3%–35%) than outdoor grazing (4.5–11.6%) [2]. Globally, 252–370 million cattle (17.5%–25.8%), 231–369 million sheep (21.1%–30.7%) and 191–283 million goats (20.5%–30.4%) could experience 10–20 additional extreme HS days per year relative to historical baselines [3].

The financial impacts are severe: projected production losses range from 3.7% to 9.8% of the baseline cattle milk and meat value [4], while goats exhibit a 3%–10% drop in milk yield and 4% in meat production [5]. These trends threaten outdoor livestock viability, particularly in lower latitudes of low- and middle-income countries (LMICs) where high adaptation costs act as economic barriers [3]. This highlights the need for tailored, region- and system-specific resilience measures across genetics, nutrition, and engineering (including nature-based) interventions. This broadly involves discussions on assorted nutritional interventions, genetic interventions, and environmental (engineered and nature-based) solutions. Therefore, this mini-review discusses recent evidence on nutritional, genetic, and engineering strategies to mitigate the impacts of HS and build climate-resilient ruminant livestock production systems globally in both intensive and extensive settings.

Adaptation and mitigation through nutrition

Nutritional interventions seek to manage the primary physiological responses to HS: reduced feed intake,

reduced respiration rate, and the redistribution of blood from the viscera to the periphery to dissipate heat [6]. Feeding highly digestible, high-energy diets can maintain productivity while minimizing the heat increment of feeding. However, high inclusion rates of rapidly fermentable grains can increase the risk of HS as their rapid fermentation results in an increase in rumen temperature compared to more slowly fermentable grains such as maize [7,8]. Slowing fermentation via chemical treatments or incorporating plant-derived polyphenols, which reversibly bind protein and decrease rumen protein degradation, can buffer this risk [9,10].

Recent research focuses on mitigating metabolic and oxidative stress using specific feed additives, though their responses can be highly inconsistent and dose-dependent.

- **Betaine (Tri-methyl glycine):** Cellular osmolytes are small organic molecules that help cells balance water pressure and protect internal structures from environmental stress. Acting as a cellular osmolyte, betaine minimizes the exothermic energy required for cellular ion pumping, thereby reducing maintenance energy requirements by up to 10% and lowering core body temperature by up to 0.5 °C [11,12]. However, a significant physiological paradox exists: at high doses, betaine accelerates hepatic lipid oxidation, which increases endogenous heat production and increases HS risk [13].
- **Selenium (Se):** Peripheral blood shunting during HS creates visceral ischemia and oxidative stress, causing tight-junction breakdown, increased gut permeability, and endotoxemia [14–16]. Selenium, as a cofactor for glutathione peroxidase, neutralizes reactive oxygen species (ROS), maintains intestinal integrity and protects cells from heat-induced damage [17,18]. Crucially, organic Se forms exhibit higher bioavailability and lower toxicity risks than inorganic Se. Nevertheless, the financial premium may limit adoption by smallholders.
- **Chromium (Cr):** Dietary supplementary Cr, organic or nano-forms, in lambs enhances insulin sensitivity, reducing fasting insulin and blunting lipolysis [19]. These adaptations decrease fat mobilization which is protective during HS since lipid oxidation requires more oxygen and generates more heat than glucose oxidation.

While additives can successfully offset HS production losses in intensive operations, their practical application is heavily limited by the economics of the farming system. In extensive grazing or smallholder networks in low- and middle-income countries (LMICs), high upfront capital costs or volatile supply chains could make the continuous commercial supplementation cost prohibitive. Consequently, wide-scale economic viability in

extensive system would depend on replacing imported additives with locally sourced, polyphenol-rich alternative forages and low-cost mineral blocks [20]. Ultimately, effective HS mitigation cannot follow a one-size-fits-all approach and must be tailored to the structural and financial realities of each system.

Adaptation and mitigation through genetics

Genetic adaptation offers a permanent, cumulative strategy to improve livestock thermotolerance. The mechanisms involve coat and hair characteristics (e.g., slick hair), heat shock proteins expression (HSPs), and efficient cellular ion transport (e.g., ATP1A1) [21,22]. However, clear structure trade-offs govern intensive (high-input, confined) and extensive (pasture-based, low-input) systems, reflecting differences in data availability, selection intensity, and environmental pressures.

In intensive commercial systems, genomic selection has enabled the introgression of specific thermotolerance markers without drastically compromising production. The introgression of the dominant SLICK hair gene into Holstein cattle provide shorter coats that enhance convective heat [22] and maintain production levels. For example, while the wild-type decreased milk yield by 9.9% under HS, the SLICK variant only decreased 3.3% [23]. Advanced tools such as genome-wide association studies (GWAS) and multiomics have identified additional candidate genes (e.g., HSP70, PRLR, SIK2), enabling precise marker-assisted selection. Heat Shock Protein genes like HSPA1A act as cellular thermometers and molecular chaperones to protect cells from thermal damage. Mutations in the prolactin receptor (PRLR) gene causes a short, "slick" hair coat that naturally improves heat tolerance. These systems benefit from accurate phenotyping via automated sensors and large reference populations, delivering rapid genetic gain. However, trade-offs exist, selection for heat tolerance can sometimes reduce peak productivity if not balanced carefully [24].

High-throughput genomics of *Bos Indicus* (zebu cattle) reveals unique genetic variants linked to tropical adaptation, heat tolerance, and disease resistance. Vechur and Kasaragod dwarf cattles are rare, indigenous Zebu breeds from Kerala, India, known for their tiny size, high disease resistance, and nutrient-rich milk. In extensive tropical and LMICs systems, adaptation relies more on cross-breeding with locally adapted *Bos indicus* genetics and conservation of indigenous breeds rather than high-throughput genomics. These low-input, pasture-based systems face challenges including limited pedigree recording, variable forage quality, and minimal infrastructure, making community-based or marker-assisted breeding approaches more practical in such settings [25,26]. Indigenous breeds often exhibit naturally evolved thermotolerance through smaller body size, efficient metabolism, and specific gene variants. For

example, the dwarf Vechur cattle of Kerala, India (Figure 1), demonstrate superior HS resilience compared with larger crossbreds, with lower rectal temperature rises and better physiological stability under high temperature-humidity index (THI) conditions, given their favorable variants in genes such as HSPA1A and ATP1A1 [27–29]. Similar patterns occur in small ruminants, where local goat and sheep breeds maintain productivity through heat shock protein (HSP)-mediated stress responses [30].

While genetic gains are promising, challenges remain. Genomic tools require substantial infrastructure unavailable to most smallholders; affordable marker panels are needed. Balancing thermotolerance against high production traits remains a key challenge. Combining genetics with nutritional and engineering interventions will be essential for climate-smart, resilient ruminant systems [31].

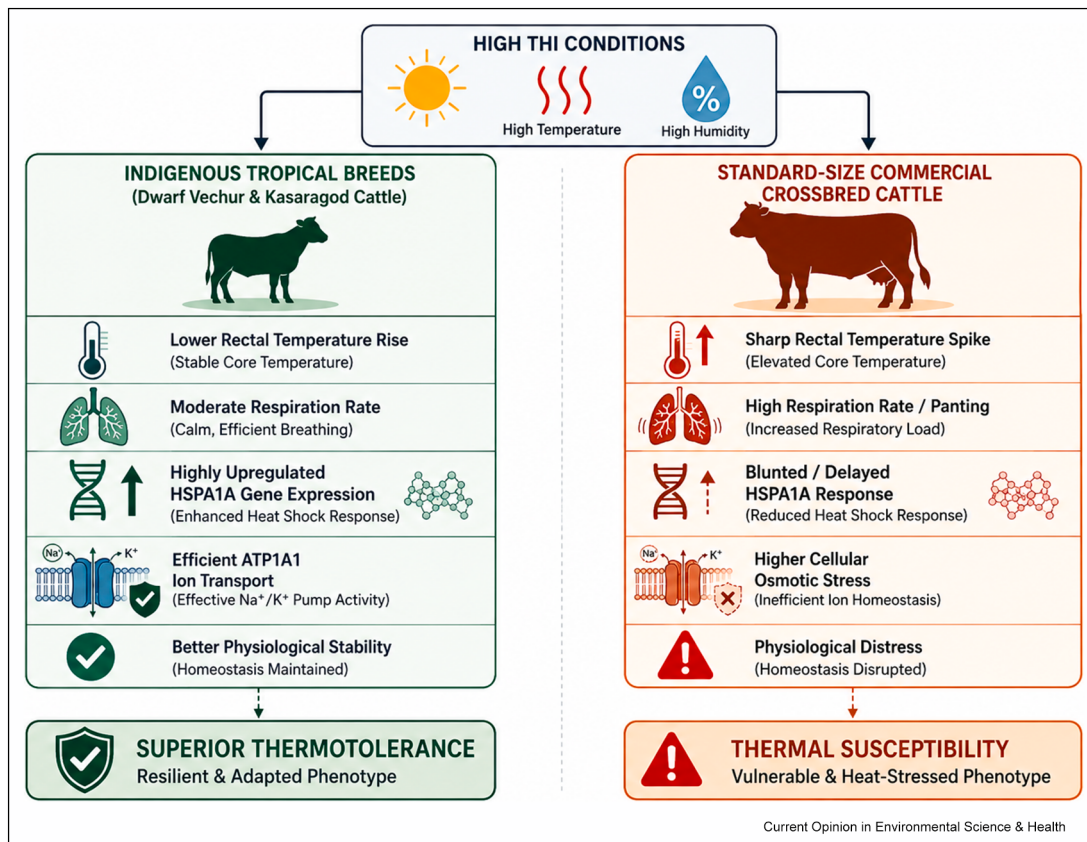
Adaptation and mitigation through engineered (including nature-based) interventions

Modifying the microclimate can be achieved through engineered interventions which can either be nature-

based or technically engineered infrastructure, with distinct regional feasibility and resource implications. Schauburger et al. [32] assessed a wide variety of adaptation measures suitable for temperate housed livestock systems including: air treatment systems (e.g. earth-air-heat exchangers), building design to reduce heat ingress and optimize heat loss (e.g. insulation and ventilation) and modification of the indoor climate at the animal level (e.g. fogging, cooling drinking water, increasing air velocity). Bashiru and Oseni [33] focused on interventions for LMICs especially those in more tropical climates where nature-based engineered solutions focused on natural shade (e.g. silvopasture) and changes to livestock management (e.g. stocking density). Table 1 summarizes the most common engineered adaptation and mitigation aligned to building design and external provision of shade and the leading pros and cons of adoption.

In extensive grazing environments, the simple provision of natural shade via native vegetation [34] planned incorporation of vegetation [e.g. hedgerows [35], silvopasture [36] represents a cost-effective tool, lowering respiration rates, body temperatures, panting scores and improved animal performance compared with unshaded

Figure 1



Comparative thermotolerance mechanisms and physiological responses of indigenous dwarf cattle (Vechur and Kasaragod) versus standard-size commercial crossbred cattle under high temperature-humidity index (THI) conditions (Image generated with AI).

Table 1

Common engineered heat stress mitigation and adaptation systems for housed and unhoused livestock.

System	Housed/Unhoused	Pros and cons	References
Natural shade (trees, hedgerows)	Unhoused	Cost effective, delivery of ecosystem services (e.g. soil health and biodiversity) but can limit feed provision (grass growth)	[37] [38] [34] [35] [36]
Artificial shade (mobile shelters, solar photovoltaic panels)	Unhoused	Easy to install or deliver diversified income but can limit feed provision	[39] [40]
Passive ventilation (building design and wind)	Housed	Well-designed natural ventilation is free but is weather dependent	[44] [43] [45]
Active ventilation (fans and mechanical ventilation)	Housed	Less wind dependent but humidity dependent (less effective in tropics)	[44] [46]
Fogging and spray cooling	Housed and unhoused	Can be effective in high humidity environments in conjunction with ventilation but water use intensive	[47] [48]
Conductive cooling	Housed	Can be effective in high humid environments but can be expensive to install. Cheaper options such as surface wetting are water use intensive	[51]

livestock for both cattle [37] and sheep [38]. Silvopasture farming is an intentional and managed system that combines trees, forage, and grazing livestock on the same land. It is a form of agroforestry that creates mutual benefits for the animals, soil, and overall farm productivity. Silvopasture (silva is forest in Latin) or wood pasture is the practice of integrating trees, forage, and the grazing of domesticated animals in a mutually beneficial way. It utilizes the principles of managed grazing, and it is one of several distinct forms of agroforestry. Properly managed silvopasture (grazed woodland) can increase overall productivity and long-term income due to the simultaneous production of tree crops, forage, and livestock. It can provide environmental benefits, and has been practiced in many parts of the world for centuries. However, an agronomic trade-off exists: dense tree canopies reduce solar radiation reaching the understory, which can lower pasture dry matter yield and alter forage quality [36].

Shade can also be provided artificially through the erection of portable covers [39], or as a by-product of enterprise diversification and layered land uses (e.g. solar photovoltaic panels) [40]. Be it natural or artificial, shade provision for all livestock systems which spend a significant amount of time outside should now be considered as a standard requirement along with water and feed access as the benefits are clear and the impacts on animal welfare and performance marked both within grazing [41] and feedlot systems [37]. However, currently the provision of shade or other heat mitigation strategies appears mixed and further research is required to identify the cost-benefit for adoption alongside stakeholder decision support and HS forecasting and monitoring tools [42].

Livestock housing design traditionally differs between temperate and tropical countries. In temperate zones livestock are typically enclosed in insulated buildings with mechanical or natural ventilation, whereas in subtropical and tropical zones the livestock buildings are generally open-sided and uninsulated. A key principle of a well-designed livestock building is to regulate internal temperature through a combination of insulation and ventilation. In humid environments, cooling requires evaporative methods, which display critical thermodynamic distinctions.

- Design and materials: Building geometry and materials [43,44], natural passive ventilation (optimized through computational fluid dynamics) [44,45], and designed mechanical active ventilation systems (e.g. fans, geothermal heat exchangers [46]) have been applied to regulate air flow and deliver cooling in modern livestock buildings. In more tropical climates further interventions are required such as fogging, surface wetting and spray cooling.
- Fogging systems: Emit an ultra-fine atmospheric mist designed to cool the ambient air via water evaporation. This system can fail under high ambient relative humidity if not accompanied with good ventilation [47] because the air is already saturated, preventing evaporation and exacerbating respiratory stress.
- Spray cooling/sprinkling: Drops large water droplets onto the animal's skin utilizing conductive and convective heat transfer via water runoff to cool the core body directly [47]. This remains highly effective in humid conditions but are resource and water use intensive.

These evaporative solutions introduce major environmental trade-offs regarding water-use efficiency and sustainability. While nature-based solutions such as

Table 2

Integrated matrix of nutritional, genetic, and engineered (including nature-based) heat stress interventions.

Intervention type	Specific strategy	Primary physiological mechanism	Example of impact	Target production system	Relative cost & ease of adoption	Key critical trade-offs & limitations
Nutritional	Dietary betaine	Osmo-protection; reduces exothermic energy spent on cellular ion pumping.	Reduction of maintenance energy requirements by up to 10% and core body temperature by up to 0.5 °C [11,12].	Intensive dairy/Confined beef.	Low-moderate cost; high ease of adoption via total mixed rations.	Paradoxical effect: Excessive doses accelerate lipid oxidation, increasing heat load.
Nutritional	Organic selenium	Glutathione peroxidase cofactor; neutralizes reactive oxygen species (ROS), preserving gut tight-junctions.	Oxidative stress index was 30% lower in supplemented sheep (2.16 ± 0.06 vs 3.12 ± 0.08 arbitrary units) during HS [17].	Universal (intensive & extensive).	Moderate cost; easily added to mineral blocks or premixes.	Higher cost relative to inorganic forms; response is highly dependent on baseline soil Se levels.
Genetic	<i>SLICK</i> gene introgression	Produces short, sleek hair coats that maximise convective and radiative heat loss.	Wild-type decreased milk yield by 9.9% under heat stress (HS), whereas the <i>SLICK</i> variant only decreased 3.3% [23].	Intensive dairy (e.g., Holstein lines).	High initial cost - breeding/genomics; simple long-term adoption.	Requires balanced selection index to avoid dilute progress in peak milk solids production.
Genetic	Indigenous breed conservation	Small body size improves surface-area-to-volume ratio; upregulated heat shock protein (<i>HSP</i>) expression.	Dwarf cattle breeds show up to 0.78 °C lower rectal temperature, 50% lower respiration and 30% lower pulse rates than crossbred cattle under HS [29].	Extensive/pastoralist (especially low- and middle-income countries [LMICs]).	Low cost; high regional compatibility but hindered by poor pedigree data.	Lower absolute milk/meat yield potentials compared to commercial crossbred lines.
Nature-based (NBS)	Silvopastoral shade	Blocks direct solar radiation; reduces animal respiration rates and panting scores.	Trees were simulated to contribute to New Zealand's milk yields by over 491 million liters and meat yields by over 8316 t annually [34].	Extensive grazing/Agroforestry.	Low-moderate capital; long-term establishment timeline.	Tree canopies reduce light penetration, potentially lowering understory pasture yield.
Technical engineered	Direct skin spray cooling	Maximizes convective and conductive heat transfer directly from the skin surface.	Spray cooling increases the total heat flux released from the skin surface of a cow by up to 162% more than that of pure convection [47].	Intensive confinement -dairy/feedlot.	Moderate-high infrastructure cost; simple automated operation.	High water footprint; elevates risks of environmental mastitis and hoof disorders due to wet bedding.
Technical engineered	Conductive cooling pads	Conducts heat directly from the animal's body to cooled stall floor surfaces.	Cows lying down on water mattresses can lose about 20%–25% of their metabolic heat by conduction [51].	Tie-stall or free-stall intensive dairies.	Prohibitively high capital cost; low variable operating costs.	Infeasible for grazing systems; requires reliable, continuous electrical grid infrastructure.

silvopasture provide carbon sequestration co-benefits through tree biomass and improved soil carbon storage, intensified mechanical cooling systems (fans, fogging, and conductive cooling) can increase on-farm energy consumption and associated greenhouse gas emissions, particularly in regions reliant on fossil fuel-based electricity. In water-scarce regions, heavy water consumption for livestock cooling creates direct conflicts with human domestic needs. To help reduce water loss, automatic wetting systems have been developed which operate based on real-time monitoring of temperature, humidity and temperature-humidity index (THI) (e.g., Ref. [48]). Nevertheless, economic development of the country and region affects the application of modern technologies and, consequently, high investment costs and lack of investment capital may delay the modernization of facilities [49].

Furthermore, prolonged operation of automated sprinklers without adequate drainage introduces animal health risks, such as increased hoof lesions and digital dermatitis due to persistently wet flooring and bedding [50], as well as elevated environmental mastitis risk from increased bacterial loads in damp conditions. Conductive cooling pads installed within stalls offer a water-free alternative, although their high capital installation costs limit their use to high-yielding dairy systems [51].

Conclusion and future perspectives

HS poses an escalating threat to global ruminant production. It also exerts profound negative effects on reproductive performance, one of the most economically sensitive traits in ruminant production, impairing oocyte quality, increasing embryonic mortality, disrupting estrus expression and hormonal profiles in females [52], and reducing semen quality, sperm motility, and fertility through oxidative damage to testicular tissue in males [53]. While nutritional, genetic, and engineered interventions each offer value, their effectiveness is highly context-dependent and involves important trade-offs in cost, productivity, water/energy use, and scalability.

Conceptual synthesis (Table 2): Nutrition delivers rapid, flexible, short-term relief (moderate cost, immediate effect but recurring input); genetics provides medium-to long-term heritable gains (high initial investment in intensive systems, lower in community breeding); nature-based and engineered solutions offer immediate environmental buffering with variable costs and co-benefits (strongest carbon and biodiversity gains from silvopasture). Synergies among the three pillars are expected to be powerful but remain insufficiently quantified.

Actionable research agenda

- Short-term (1–3 years): Low-cost integrated packages for LMICs (shade + local polyphenols +

indigenous genetics) with robust cost–benefit and water/carbon analyses.

- Medium-term (3–7 years): Affordable genomic tools and community breeding expansion to sheep, goats, and buffaloes; large-scale validation of precision monitoring.
- Long-term: Multiomics to minimize productivity–thermotolerance trade-offs and support climate-smart breeding.

Urgent coordinated action across disciplines and policy support for smallholders will be essential to safeguard ruminant production and global food security under accelerating climate change.

Authorship and contribution statement

All authors MRFL, MJR and FRD equally contributed to the conceptualization, writing, reviewing and editing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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