

Heat tolerance mechanisms in cattle—status in zebu cattle: A review

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ABSTRACT

Bos taurus cattle breeds that have evolved in temperate environments fail to fully adapt to extreme heat conditions. The better adaptation to these environments by *Bos indicus* cattle is primarily related to the greater sweating rates due to higher density and larger perimeter of sweat glands, quick transfer of metabolic heat to the skin due to a less tissue resistance and less hair coat resistance to heat loss. These characteristics permit these cattle to maintain body temperature more efficiently than *Bos taurus* breeds. At increased core body temperatures, there is increase in glucose and amino acid oxidation, decrease in fatty acid metabolism, alteration in endocrine system and activation of the stress response genes to environmental heat loads. The cellular heat shock response is another component of adaptation to heat stress. Heat stress activates heat shock transcription factor-1 (HSF1) leading to increased expression of heat shock proteins (HSP) coupled with decreased expression and synthesis of other proteins, and HSP induced activation of immune system. The central role that HSF1 has in coordinating thermal tolerance suggests that there is opportunity to improve thermal tolerance via gene manipulation. Determining the basis of heat tolerance, especially the *Bos indicus* including Indian zebu cattle breeds will lead to opportunities for optimum utilization via altered breeding and management of these magnificent genetic resources.

Key words: Cattle, Cutaneous heat loss, Cellular heat shock response, Heat tolerance

Heat stress is a particularly severe problem in high yielding milch, dual purpose animals as well as drought cattle population. Over 50% of the bovine population is located in the tropics. It has been estimated that heat stress causes severe economic loss in approximately 60% of the dairy farms around the world (Wolfenson *et al.* 2000). The magnitude of the effect of heat stress on reproduction in dairy cattle is increasing as higher milk yield leaves the animals more susceptible to the deleterious effects of heat stress (Al-Katanani *et al.* 1999, Lopez-Gatius 2003).

As compared to temperate cattle breeds (*Bos taurus*), zebu cattle breeds (*Bos indicus*) including Indian breeds can better withstand high temperatures (Seif *et al.* 1979, Srivastva and Sidhu 1979, Singh and Mishra 1980, Lemerle and Goddard 1986, Khan 1986, Meirelles *et al.* 1999). They experience less severe reduction in feed intake (Allen *et al.* 1963, Johnston *et al.* 1958, Seif *et al.* 1979), growth rate (Rajaratne *et al.* 1983), milk yield (Johnson 1965, DeVillalobos *et al.* 1975), work capacity (Upadhyay and Madan 1987, Carvalho *et al.* 1995) and reproductive function (Johnston *et al.* 1963, Skinner and Louw 1966, Anonymous 1980, Rocha *et al.* 1998, Barros 2002, Paula-Lopes *et al.* 2003, Eberhardt 2005)

in response to heat stress. The crossing of zebu cattle with temperate breeds reduces their heat tolerance capacity and the effect of heat on various traits increases with decrease in zebu inheritance (Garcia *et al.* 1979, Holmes *et al.* 1980, Singh and Mishra 1980, Martinez-Santisteban *et al.* 1984, Morais 1985b, Upadhyay and Madan 1987). This article reviews the present knowledge in literature about heat tolerance mechanisms in cattle per se vis-a-vis current understanding about better heat bearing capacity of zebu cattle.

Cutaneous heat loss

The ability of the animals to maintain normal body temperatures by cutaneous and respiratory heat dissipation plays a predominant role in adaptation of cattle in hot climate (Gebremedhin and Wu 2001). They are able to maintain body core temperature until skin surface temperature exceeds 35°C (Pollard *et al.* 2005). Above this surface temperature, cows begin to store heat, rectal temperature rises and cutaneous heat loss plays the major role in body temperature control mechanism besides increased respiration rates (DeVillalobos *et al.* 1975, Pollard *et al.* 2004). The variation in cutaneous heat loss between cows is much greater above 35°C and the probable reason is might be due to the differences in hair coat characteristics, numbers as well as activity of sweat

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glands and regulation of epidermal vascular supply (Olson *et al.* 2006).

The hair coat density and thickness, hair length and colour and skin color are the major coat characteristics affecting efficacy of heat loss from the skin surface. Factors like absorption of solar radiation due to skin and hair coat colour and hair coat density (which affects airflow over the skin surface) influence heat loss (DaSilva *et al.* 2003). Several findings on these aspects have indicated significant variation among various breeds of different origin (Mohan and Prabhu 1969, DeVillalobos *et al.* 1975, Srivastva and Sidhu 1979, Nagarcenkar and Sethi 1981, King *et al.* 1988). The especially high heat-retaining properties of a comparatively thick natural coat of hair in most taurus cattle breeds than zebu breeds suggests the special need to select animals of low coat score for the hot and humid tropics (Yeats and Partridge 1975, Yeats 1977). Even the zebu crossbreds with shorter (length) and thinner (diameter) hair length and lighter (weight) hair coats show less increase in rectal temperatures than purebred European breeds when exposed to higher environmental temperature (Morais 1985a, Morais 1986, Holmes *et al.* 1980).

The cattle have an apocrine sweat gland with one sweat gland associated with each hair fibre. Thus, hair density directly affects the number of sweat glands, and hair diameter and length have effects on heat loss by regulating airflow at the skin surface (Gebremedhin and Wu 2001, Olson *et al.* 2006). Strong correlation of the sweat gland number and sweating volume with heat adaptation of cattle breeds has been observed (Domingues 1961, Nagarcenkar and Sethi 1981). The zebu cattle including the Indian cattle breeds like Sahiwal, Tharparker, Red Sindhi etc. has the higher number of sweat gland per unit area and larger sweat gland perimeter resulting in higher sweating response compared to exotic breeds like Brown Swiss, Freisian, Jersey etc. (Branton *et al.* 1966, Singh *et al.* 1977, Govindaiah *et al.* 1980). There is reduction in density of sweat glands in crossbred cattle and this reduction is proportional to reduction in zebu inheritance (Taneja 1960, Branton *et al.* 1966, Jenkinson and Nay 1973, Govindaiah *et al.* 1980, Finch *et al.* 1982, Bhayani and Vyas 1989, Carvalho *et al.* 1995). The body temperature in temperate *Bos taurus* cattle may also be influenced by a lower capacity of the animals to redirect blood (which carries heat) from internal organs to the capillary beds in the skin and thereby increase heat dissipation (Finch 1986). Curvilinear models indicate that the Brahman and Shorthorn crossbreds have not yet attained the maximum sweating response, when the sweating response of Shorthorn cattle start approaching plateau under same stress conditions (Finch *et al.* 1982). The large variability in cutaneous heat loss between zebu and taurus cattle breeds suggest that there is opportunity to utilize better cutaneous heat loss abilities of zebu breeds including Indian cattle breeds in dairy cattle breeding programmes.

The genes affecting hair and skin color as well as hair

length and density have been identified in cattle (Klungland and Vage 2003, Olson *et al.* 2003, Olson *et al.* 2006, Mariasegaram *et al.* 2007). One such gene is the slick hair gene, which controls hair length. Originally described in Senepol cattle, the gene was subsequently identified in Carora cattle (Olson *et al.* 2003). The gene has been mapped to chromosome 20 (Mariasegaram *et al.* 2007). Animals with the dominant allele have a very short, sleek, and sometimes glossy coat. Cattle with slick hair coats experience lower body temperatures in heat stress conditions (Dikmen *et al.* 2008). Besides slick hair gene, investigations for genetics of white spotting has confirmed role of QTL regions covering the *KIT* (receptor tyrosine kinase) locus on BTA6 and *MITF* (microphthalmia associated transcription factor) gene on BTA18 (Liu *et al.* 2009). Further investigations are required to identify the genes involved in regulation of sweat gland function in cattle.

Endocrine response

Since, the endocrine system plays an important role in adaptation to environmental stress, it is not surprising that thermal stress has a profound effect on circulating hormones (Johnson and Vanjonack 1976, Collier *et al.* 1982). The levels of prolactin, glucocorticoids and thyroid hormones are well known to be altered in response to thermal stress.

Prolactin, a hormone important for galactopoiesis and lactational persistency, is elevated during thermal stress although the mechanistic basis is not well understood. Alteration in prolactin secretion is associated with altered metabolic state of heat stressed animals. One possibility is that prolactin is involved in meeting increased water and electrolyte demands of heat-stressed cows (Collier *et al.* 1982). Collectively these results suggest that elevated prolactin and decreased aldosterone concentrations in heat-stressed cattle may be involved in meeting electrolyte and water requirements during thermal stress (Collier *et al.* 1982).

Thyroxine (Collier *et al.* 1982) and some other hormones associated with metabolism like glucocorticoids (Alvarez and Johnson 1973, Niles *et al.* 1980, Swenson 1977) and growth hormone (Mitra *et al.* 1972) tend to be reduced in plasma of chronically heat stressed cattle. The reduction in concentrations of these hormones may be associated with metabolic adaptation of cattle to chronic thermal stress. The hyperthermia depresses thyroid function resulting in reduction in the metabolic heat generation. Though, concentrations of thyroid hormones are higher in *Bos indicus* animals than in *Bos taurus* under normal feeding conditions (Christopherson *et al.* 1979, O'Kelly and Spiers 1994, Rastogi and Aggarwal 1990, Rehman and Roychaudhury 1996, Kroupova *et al.* 1996). However, the thyroid hormone concentrations are significantly lower in *Bos indicus* animals than in *Bos taurus* after 72 h starvation but did not differ significantly between breeds after 96 h starvation. This suggests that the differences in plasma concentrations of

thyroid hormones of *Bos indicus* and *Bos taurus* in a thermoneutral environment originate from quantitative differences in the supply of nutrients from the rumen to body tissues (O'Kelly and Spiers 1994).

The tropically adapted *Bos indicus* breeds show increased adrenocortical functions besides low thyroid function compared to and *Bos taurus* breeds suggesting that metabolic factors associated with tolerance of stressful conditions, including high temperatures, are related to low growth rates and vice versa, so that selection for growth rate could lead to impaired heat tolerance (Van-der-Westhuisen 1979, Johnson and Vanjonack 1976).

Besides these three hormones IGF-I is also expressed at lower levels during heat stress. During periods of negative energy balance such as malnutrition or when the energy demands of milk production exceeds energy intake (i.e. early lactation), the somatotrophic axis becomes uncoupled when circulating somatotropin concentrations rise and plasma IGF-I concentrations fall (Bauman and Vernon 1993). However, no differences are observed in mean growth hormone concentrations, growth hormone pulsatility characteristics, or growth hormone response to growth hormone releasing factor in heat-stressed versus pair-fed thermoneutral controls (Rhoads *et al.* 2007). Heat stress, independent of reduced feed intake, decreases the abundance of the growth hormone receptors; however, both heat shock and malnutrition are sufficient to decrease signal transducer and activator of transcription (STAT)-5 phosphorylation (Rhoads *et al.* 2007). Consistent with reduced growth hormone signaling through STAT-5, hepatic IGF-I mRNA abundance is lower in heat shock and underfed thermoneutral animals. Thus, the reduced hepatic responsiveness (in terms of IGF-I gene expression) observed during heat shock appears to involve mechanisms associated with a reduction in feed intake. The physiological significance of reduced hepatic growth hormone receptor abundance during heat shock is unclear at this time but may serve to alter other growth hormone-dependent hepatic processes such as regulation of gluconeogenesis.

Metabolic changes during heat stress

Increased heat load decreases nutrient uptake in almost all species and in case of cattle, the nutrient uptake decreases up to about 30% of dry matter intake as heat load increases (West 1999). It is traditionally assumed that decreased DMI is primarily responsible for reduced milk yield. The reduced nutrient intake accounts for about 40% reduction in the milk yield and it is hypothesized that changes in carbohydrate metabolism are responsible for a large portion of the remainder (Fuquay 1981, West 1999, Wheelock *et al.* 2006, Rhoads *et al.* 2007).

The heat stress also markedly alters glucose homeostasis in heat-stressed cows. There is increased glucose disposal into cells in heat-stressed compared with pair-fed thermal

neutral cows (Wheelock *et al.* 2006). Glucose disposal differences can be reconciled by a weaker insulin response to the glucose bolus by the pair-fed thermal neutral cows, whereas the insulin response remains unchanged during heat stress. Despite similar nutrient intake, the pair-fed thermal neutral control group appears to reduce insulin-dependent glucose utilization, whereas the heat exposed group maintains insulin-dependent glucose utilization. The feed restriction during thermal neutral conditions stimulated the expression of PGC-1 α , PEPCK, and pyruvate carboxylase (PC). In contrast, discordant changes (PC increased but PGC-1 α and PEPCK were unaltered) in gluconeogenic gene expression was evident during heat stress (Wheelock *et al.* 2006) indicating that hepatic adaptation to reduced nutrient intake, in terms of glucose metabolism, differs with variations in environmental temperature.

Cellular heat shock response

Exposing the cells to elevated temperature leads to a general inhibition of protein synthesis, defects in protein structure and function, morphological changes due to cytoskeleton rearrangements, shifts in metabolism, alterations in cell membrane dynamics and fluidity, and decreases in cell proliferation (Sonna *et al.* 2002). These anomalies invoke large changes in gene transcription and protein synthesis known as the heat shock response (Lanks 1986, Lindquist 1986).

A transcription factor family known as the heat shock factor (HSF) has been implicated as important first responders during the onset of elevated cell temperature (Trinklein *et al.* 2004, Page *et al.* 2006). Although mammals express HSF1, 2, and 4, HSF1 is primarily responsible for inducing heat shock protein (HSP) gene expression during hyperthermia (Pirkkala *et al.* 2001). The current model of HSF1 transcriptional activity indicates that nonstressed cells contain folded HSF1 monomers bound to HSP within the cytoplasm. Upon heat stimulus, the HSP dissociate from HSF1 monomers, which then unfold and bind to two other HSF1 monomers to form trimers before their nuclear translocation. Once in the nucleus, homotrimeric HSF1 binds promoters containing heat shock elements (HSE) to activate heat stress target gene transcription. Although HSF1 has traditionally only been associated with regulation of HSP, recent evidence now links it to regulation of carbohydrate metabolism, transport, cytoskeleton, and ubiquitination during heat shock (Page *et al.* 2006). The HSF1 gene has been mapped to chromosome 14 in cattle (Winter *et al.* 2007), however, investigations of HSF1 regulation and function are limited in bovine species despite the importance of HSF1 to the initiation of the heat shock response.

Microarray analysis utilizing bovine-specific cDNA arrays obtained from the National Bovine Functional Genomics Consortium, USA (Suchyta *et al.* 2003) profiled bovine mammary epithelial cell (BMEC) gene expression in

response to acute heat stress using an *in vitro* system that closely approximates mammary development and function (Collier *et al.* 2006). During the initial period of hyperthermia (42°C), the BMEC exhibited morphological changes (regression of ductal branches) and reduced cell growth. Consistent with these physical alterations in cell behavior, gene transcripts associated with protein synthesis and cellular metabolism were downregulated.

The HSP 70 gene expression in BMEC remains elevated for 4 h at 42°C before returning to basal levels 8 h later, signaling the end of thermotolerance and activation of genes associated with apoptosis (Collier *et al.* 2006). The prostaglandin A1 (PGA1) induces HSP synthesis in bovine mammary epithelial cells resulting in protection against cellular stresses (Collier *et al.* 2007).

Impact of endocrine system on cellular heat shock response

The process of acclimation is under endocrine regulation. A variety of endocrine or paracrine signals associated with a range of stressors modify the intracellular heat shock response. The melatonin and prolactin also upregulate HSP 70 gene expression in bovine mammary epithelial cells during heat shock, whereas leptin downregulates its expression. PGA1 increases HSP gene expression via increased HSF1 activation. However, little is known about how other hormones play the role in HSP gene expression.

Two hormones are known to increase in plasma with response to thermal stress (prolactin and glucocorticoids) and they are associated with modifying the intracellular heat shock response. When glucocorticoids enter the cytoplasm, they cause the release of preformed cytoplasmic HSP 70 and 90, which are bound to the glucocorticoid receptor. Release of the HSP in response to increased glucocorticoid binding to its receptor provides an instant pool of HSP to protect against protein denaturation (Vijayan *et al.* 2003). Prolactin also modifies HSP gene expression, although the mechanism is unknown and prolactin's role in seasonal changes in cognate and inducible forms of HSP 70 remains to be determined.

Future action plan

As the demand for milk is increasing day by day, more emphasis is on increasing productivity by intensification through selection or crossbreeding local cattle population with high yielding temperate breeds. However, the high yielding animals in general and temperate breeds in particular experience severe reduction in production, reproduction and growth parameters during hot and humid conditions. Heat tolerance is considered to be one of the most important adaptive aspects for Indian cattle breeds. The ability of the crossbred animals to withstand heat, resulting from crossing of high yielding temperate breeds with the tropically adapted Indian cattle population, is reduced in proportion to decrease in zebu inheritance. The lack of thermal tolerance at desired

levels is one of the major constraints in evolving high yielding cattle breed suited to environmental conditions of our country. Taking advantage of heat adapting abilities of cattle breeds from our country, like Kankrej, Krishna Valley, Nellore, Ongole and Gir, have been used extensively in breeding programmes designed to evolve cattle suited for tropical areas in North and South American countries besides Australia since 18th century (Johnston *et al.* 1958, Bhushan 2006). Early identification of best heat tolerant animals within heat tolerant breeds and also heat tolerant animals within a non-tolerant breed becomes prerequisite for such breeding programmes. However, early identification of heat tolerant animals is not easy under field conditions. An in-depth understanding of genes and mechanisms involved in regulating sweat gland function, endocrine changes during thermal exposure and cellular heat shock response in zebu cattle would enable us to exploit their heat tolerance capacities in more fruitful manner leading to evolution of breeding programmes designed to produce a breed of cow incorporating the required production characteristics of high yielding temperate cattle breeds and the heat tolerance or other desired traits of indigenous zebu cattle breeds. Further, under changing environmental conditions due to global warming, such animals will be required not only in our country, but they can also generate valuable foreign exchange by exporting their germplasm to other needy countries as well.

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