Physiological and cellular adaptations of zebu cattle to thermal stress

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Abstract

During their separate evolution from *Bos taurus*, zebu cattle (*Bos indicus*) have acquired genes that confer thermotolerance at the physiological and cellular levels. Cattle from zebu breeds are better able to regulate body temperature in response to heat stress than are cattle from a variety of *B. taurus* breeds of European origin. Moreover, exposure to elevated temperature has less deleterious effects on cells from zebu cattle than on cells from European breeds. Superior ability for regulation of body temperature during heat stress is the result of lower metabolic rates as well as increased capacity for heat loss. As compared to European breeds, tissue resistance to heat flow from the body core to the skin is lower for zebu cattle while sweat glands are larger. Properties of the hair coat in zebu cattle enhance conductive and convective heat loss and reduce absorption of solar radiation. At the cellular level, genetic adaptations to resist deleterious effects of elevated temperature result in preimplantation embryos from zebu being less likely to be inhibited in development by elevated temperature than are embryos from European breeds. The zebu genotype has been utilized in crossbreeding systems to develop cattle for beef and dairy production systems in hot climates but success has been limited by other unfavorable genetic characteristics of these cattle. An alternative scheme is to incorporate specific thermotolerance genes from zebu cattle into European breeds while avoiding undesirable genes. Once specific genes responsible for thermotolerance in zebu have been identified or mapped, breeding strategies such as marker-assisted selection and transgenics can be applied to further the exploitation of the zebu genotype for cattle production systems.
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1. Introduction—the zebu as a genetic resource for thermotolerance genes

While the humped cattle of Indian origin (*Bos indicus* or zebu cattle) and the generally-humpless cattle of Europe and Africa (*Bos taurus*) arose from a common ancestor, these two

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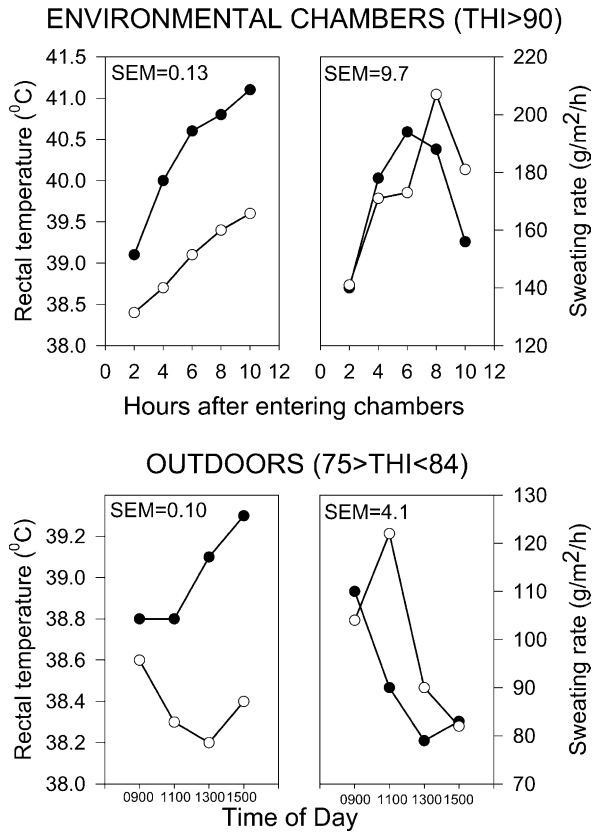*E-mail address:* hansen@animal.ufl.edu (P.J. Hansen).

Fig. 1. Differences between Hereford (closed circles) and Brahman (open circles) in regulation of rectal temperature and sweating rate. Data are redrawn from Gaughan et al. (1999).

subspecies have undergone separate evolution for several hundred thousand years. Analysis of mitochondrial DNA sequences and microsatellite loci indicate that *B. indicus* diverged from *B. taurus* somewhere between 110,000 and 850,000 years ago (Bradley et al., 1996; MacHugh et al., 1997). Among the genetic adaptations that have developed in zebu cattle during its evolution have been the acquisition of genes for thermotolerance. As illustrated in Fig. 1, cattle from zebu breeds are better able to regulate body temperature in response to heat stress than are cattle from a variety of *B. taurus* breeds of European origin (McDowell et al., 1953; Cartwright, 1955; Allen et al., 1963; Finch, 1986; Carvalho et al., 1995; Hammond et al., 1996; Gaughan et al., 1999). Genetic differences in thermotolerance extend to the cellular level as well because deleterious effects of elevated temperature on cellular function are less for cells from Brahman cattle than cells from Angus and Holstein (Malayer and Hansen, 1990; Kamwanja et al., 1994; Paula-Lopes et al., 2003; Hernández-Cerón et al., 2004).

　　Because zebu cattle are thermotolerant, the consequences of exposure to heat stress for production of milk and meat are less for *B. indicus* than for European *B. taurus* breeds. Thus, as compared to breeds of European origin, zebu cattle experience less severe reduc-

tions in feed intake (Kibler and Brody, 1951; Johnston et al., 1958; Allen et al., 1963; Seif et al., 1979), growth rate (O'Bannon et al., 1955, Cartwright, 1955), milk yield (Johnson, 1965) and reproductive function (Johnston et al., 1963; Skinner and Louw, 1966; Rocha et al., 1998) in response to heat stress. The objective of this review is to outline the current understanding of the biological mechanisms which make zebu cattle adapted for regulation of body temperature during heat stress and for maintenance of cellular function when hyperthermia ensues.

2. Adaptations in zebu cattle that confer ability to regulate body temperature during heat stress

2.1. Thermoregulatory mechanisms in cattle

Like for other homeotherms, cattle regulate internal body temperature by matching the amount of heat produced through metabolism with the heat flow from the animal to the surrounding environment. Heat flow occurs through processes dependent on surrounding temperature (sensible heat loss; i.e. conduction, convection, radiation) and humidity (latent heat loss; evaporation through sweating and panting). The magnitude of sensible heat loss via conduction and convection is dependent on the surface area per unit body weight, the magnitude of the temperature gradient between the animal and the air, and the conductance of heat from the body core to the skin and from the skin to the surrounding air. Heat exchange by radiation depends upon surface area as well as the reflective properties of the hair coat. Light-colored hair coats and hair coats that are sleek and shiny reflect a greater proportion of incident solar radiation than hair coats that are dark in color or more dense and wooly (Stewart, 1953; Hutchinson and Brown, 1969; Finch, 1986; Hansen, 1990).

One physiological response to heat stress is a reduction in heat production (Kibler and Brody, 1951; Seif et al., 1979), which in turn is caused in large part by a reduction in feed intake (Kibler and Brody, 1951; Johnston et al., 1958; Seif et al., 1979; Lough et al., 1990), milk yield (Johnson, 1965; Lough et al., 1990; Elvinger et al., 1992), and thyroid hormone secretion (Magdub et al., 1982; Al-Haidary et al., 2001). Heat stress also leads to activation of heat loss mechanisms. Blood flow to the periphery increases so that heat loss via conduction and convection is enhanced (Choshniak et al., 1982). Cattle change posture and orientation to the sun to reduce gain of heat from solar radiation. Moreover, chronic exposure to elevated environmental temperatures results in a lightening of the hair coat (Stewart and Brody, 1954). Heat stress also leads to activation of evaporative heat loss mechanisms involving an increase in sweating rate and respiratory minute volume (Kibler and Brody, 1952; Choshniak et al., 1982; Gaughan et al., 1999; Al-Haidary et al., 2001). About 70–85% of maximal heat loss via evaporation is due to sweating with the remainder due to respiration (Kibler and Brody, 1952; Finch, 1986). As air temperatures approach those of skin temperature, evaporation becomes the major route for heat exchange with the environment.

2.2. Differences between zebu and European breeds

It follows from the discussion above that the superior thermoregulatory ability of zebu cattle as compared to European breeds must be the result of reduced heat production,

increased capacity for loss of heat to the environment, or some combination of both. Clearly, low metabolic rates resulting from reduced growth rates and milk yields of many zebu breeds is a major contributing factor to thermotolerance. There is also evidence that the basal metabolic rate of *B. indicus* is lower than for *B. taurus*. For example, the heat production rate per unit surface area in non-lactating and fasting cows was estimated at $100 \, \text{Mcal/m}^2$ for Holstein, $75 \, \text{Mcal/m}^2$ for Jersey and $57 \, \text{Mcal/m}^2$ for Red Sindhi $\times$ Holstein (Johnston et al., 1958). Similarly, resting heat production of Hariana cattle was less on a metabolic body weight basis than for F_1 crosses of Hariana with Holstein, Jersey, or Brown Swiss (Singh and Bhattacharyya, 1985). Maintenance requirements for Brahman $\times$ Hereford and Hereford $\times$ Brahman cows were less than for crossbreds between *B. taurus* breeds (Reid et al., 1991). One possible reason for reduced metabolic rates in *B. indicus* is reduced size of internal organs as was shown by comparisons of the relative size of the digestive system of Red Sindhi $\times$ Holstein and Red Sindhi $\times$ Jersey with digestive system size in Holstein and Jersey (Swett et al., 1961).

Properties of the skin explain much of the thermotolerance of zebu cattle. Finch (1985) found that the tissue resistance to heat flow from the body core to the skin was lower for Brahman cattle than for Shorthorn cattle at high air temperatures. The physiological basis for this difference has not been identified. One possibility is that the density of arteriovenous anastomoses is higher in *B. indicus*. These structures, which have lower resistance to flow than vascular passages involving capillary networks, facilitate increased blood flow to the skin during heat stress (Hales et al., 1978). While zebu cattle have reduced resistance of heat flow from the body core to the skin than European breeds, the converse is true when considering flow of heat from the skin to the surrounding air. As cited by Finch (1986), Gatenby (1979) found that the resistance to heat flow in the coat for cattle standing in the sun was 116 s/m for Boran and 15 s/m for Hereford. Thick and dense hair coats, such as are typical of many *B. taurus*, reduce heat flow via conduction and convection and exacerbate effects of heat stress (Berry and Shanklin, 1961; Finch et al., 1984). Clipping the hair of Shorthorn cattle reduced the magnitude of hyperthermia in response to heat stress (O'Bannon et al., 1955). The smooth and shiny hair coats of zebu cattle also act to reduce heat exchange via radiation (Hutchinson and Brown, 1969). Many *B. indicus* breeds have hair of light color that reflects a large proportion of incident solar radiation (Stewart and Brody, 1954; Hutchinson and Brown, 1969; Finch et al., 1984). Cattle exposed chronically to high temperature become progressively lighter in color and there is some evidence that this change occurs more rapidly for Brahman than for Brown Swiss or Jersey (Stewart et al., 1951; Stewart and Brody, 1954).

Zebu cattle have been reported to have a higher density of sweat glands than European breeds (Nay and Heyman, 1956) although there was no difference in sweat gland density between Sahiwal and Jersey (Pan, 1963). Moreover, sweat glands of *B. indicus* have been reported to be larger in size (Dowling, 1955; Nay and Heyman, 1956; Pan, 1963), to be closer to the surface of the skin (Dowling, 1955) and to have more layers of cells in the epithelial layer (Carvalho et al., 1995) than of *B. taurus*. The importance of these differences in sweat glands for the superior thermotolerance of *B. indicus* is not clear. In several studies (Allen, 1962; Allen et al., 1963; Gaughan et al., 1999), sweating rate was greater for zebu cattle than European cattle (see Fig. 1 for illustration). In other studies, however, maximum sweating rate did not differ between zebu and European breeds (Kibler and Brody, 1952;

Allen, 1962). In fact, sweating rate during heat stress can be greater for unadapted *B. taurus* breeds (Kibler and Brody, 1952; Thompson et al., 1953; Finch, 1985), probably because differences in other thermoregulatory mechanisms mean that *B. taurus* require more evaporative heat loss to maintain homeothermy.

The actual rate of heat loss via sweating depends not only upon the extrusion of water at the skin surface but also upon the evaporation of that water. In an early study, Thompson et al. (1953) observed that evaporative heat loss rates were less affected by humidity for Brahman cows than for Holstein and Brown Swiss cows. More recently, Finch (1985) reported that sweating rate in Brahman cattle exposed to heat stress was unaffected by humidity of the surrounding air while sweating rate of Shorthorn cattle was reduced as humidity increased. This result was interpreted as reflecting the greater trapping of humidified air in the dense hair coat of the Shorthorns.

There is no evidence that respiratory capacity for heat loss is superior for zebu cattle. The proportion of evaporative heat lost via respiration was roughly similar for Brahman, Holstein, Jersey and Brown Swiss (Kibler and Brody, 1952). During heat stress, evaporative heat loss via respiration rate can be greater for European breeds (Kibler and Brody, 1952; Cartwright, 1955; Seif et al., 1979; Gaughan et al., 1999) and this occurrence also probably reflects the greater engagement of heat loss mechanisms for the less-adapted breeds.

It is often thought that the appendages on zebu cattle are an important reason for the superior thermoregulatory ability of these cattle since they increase the surface area per unit body weight as compared to *B. taurus*. The actual importance of these anatomical features is not likely to be crucial for thermoregulation, however, because surgical removal of the dewlap or hump of Red Sindhi bulls did not have a significant effect on thermoregulatory ability (McDowell, 1958; McDowell et al., 1958). Additionally, differences in regulation of rectal temperature in response to heat stress were observed between Jersey and Red Sindhi × Jersey even though surface area per unit body weight or metabolic body weight was similar between the two genotypes (McDowell et al., 1953).

Heat stress has less severe effects on semen quality of zebu bulls than it does on bulls of European breeds (Johnston et al., 1963; Skinner and Louw, 1966) and this phenomenon reflects not only adaptations that affect whole-body thermoregulation but also specific adaptations that enhance the local cooling of blood entering the testis. This conclusion is based on results of a recent study by Brito et al. (2004) who compared anatomical features of the testicular thermoregulatory system between Nelore, crossbred (5/8 or 5/16 Charolais × zebu), and Angus bulls. Among their findings was the observation that the ratio of testicular artery length to testicular volume was greatest for Nelore bulls, intermediate for crossbred bulls and least for Angus bulls. Testicular artery wall thickness and the distance between arterial–venous blood in the testicular vascular cone was least in Nelore, intermediate in crossbreds and greatest in Angus. As would be expected from such anatomical differences, testicular intra-arterial temperature was lowest in Nelore, intermediate in crossbreds and highest in Angus.

3. Cellular resistance to elevated temperature

Much of the reduction in productive performance of cattle in response to heat stress is a reflection of the homeokinetic changes animals undergo in an attempt to regulate body
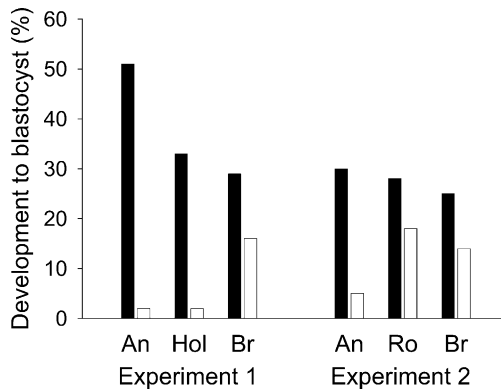
Fig. 2. Genetic differences in the deleterious effects of elevated culture temperature on subsequent embryonic development. Embryos > 8 cells at day 4 after insemination were cultured at either 38.5° continuously (solid bars) or at 41 °C for 6 h followed by 38.5 °C thereafter (open bars). The proportion of embryos that became blastocysts was determined at day 8 after fertilization. Data from Experiment 1 are redrawn from Paula-Lopes et al. (2003) and data from Experiment 2 are redrawn from Hernández-Cerón et al. (2004).

temperature. For example, the reduction in growth rate and milk yield in heat-stressed cattle is probably caused largely by the decrease in feed intake. Provision of supplemental feed through a rumen fistula reduced the decline in milk yield in heat-stressed cows (Johnson et al., 1961) while restriction of feed intake in cows at thermoneutral temperatures reduced milk yield to values comparable to heat-stressed cows (Lough et al., 1990). Nonetheless, the hyperthermia resulting from heat stress can also compromise cellular function and result in physiological changes inimical to animal production. This is particularly true for reproduction: elevations in testicular temperature impede spermatogenesis (Setchell, 1978) and culture of oocytes and embryos at temperatures characteristic of those experienced by heat-stressed cows can compromise subsequent embryonic development (Rivera and Hansen, 2001; Krininger et al., 2003; Roth and Hansen, 2004).

There is evidence that cattle that evolved in hot climates have acquired genes that protect cells from the deleterious actions of elevated temperature. Genetic resistance to cellular effects of elevated temperature are seen in both *B. indicus* as well as two New World breeds of *B. taurus*, the Senepol and Romosinuano. Thus, for example, the decrease in lymphocyte viability caused by heat shock was greater for lymphocytes from Angus cows than for lymphocytes from Brahman and Senepol cows (Kamwanja et al., 1994). Likewise, lymphocytes from Brahman and Senepol cows were more resistant to heat-induced apoptosis than lymphocytes from Angus and Holstein cows (Paula-Lopes et al., 2003). As illustrated in Fig. 2, short-term exposure of embryos to elevated temperature causes a less severe reduction in development for Brahman and Romosinuano embryos than for Angus or Holstein embryos (Paula-Lopes et al., 2003; Hernández-Cerón et al., 2004). There were also differences between Brahman and Holstein in endometrial responses to culture at elevated temperature (Malayer and Hansen, 1990).

The finding that there are genetic differences in cellular resistance to elevated temperature in cattle is the first example in endotherms of genetic adaptations in cellular resistance to elevated temperature. It is possible that the same gene or genes conferring cellular ther-

motolerance are present in Brahman, Senepol, and Romosinuano, especially because of the contribution of *B. indicus* genotypes to New World cattle breeds (Magee et al., 2002). An alternative explanation is that distinct thermotolerance genes are present in the different genotypes. Identification of the genes conferring cellular thermotolerance offers the possibility of transferring these genes to heat-sensitive breeds to improve reproduction and other phsyiological systems compromised by hyperthermia.

At present, little is known regarding the molecular basis for the improved cellular resistance to elevated temperature in thermotolerant cattle. There were no significant differences between Brahman, Senepol and Angus in the amount of heat shock protein 70 (HSP70) in heat-shocked lymphocytes (Kamwanja et al., 1994) although the non-significant tendency for lower amounts in Brahman and Senepol may indicate that protein denaturation in response to elevated temperature (one of the signals for HSP70 synthesis; Ananthan et al., 1986), is reduced in Brahman and Senepol. The capacity for transcription in response to elevated temperature seems to be important for expression of genetic differences because there were no differences between Brahman and Holstein embryos in resistance to elevated temperature at the two-cell stage (Krininger et al., 2003), a time when the embryonic genome is largely inactive (Memili and First, 2000). Also, in vitro effects of elevated temperature on spermatozoa were similar for Brahman, Brahman-influenced breeds, Angus, and Holstein (Chandolia et al., 1999).

It is unlikely that inseminating European breeds of cattle with semen from *B. indicus* to produce thermotolerant embryos will be effective in improving fertility during heat stress. Not only are genetic differences in cellular resistance to elevated temperature not expressed at the two-cell stage (Krininger et al., 2003), a time when embryos are very sensitive to elevated temperature (Edwards and Hansen, 1997; Krininger et al., 2003), but the cellular thermotolerance of crossbred embryos is dependent upon the genotype of the oocyte and not the spermatozoa. Embryos produced by insemination of Brahman oocytes with Angus spermatozoa were more thermotolerant than embryos produced by insemination of Holstein oocytes with Angus semen (Block et al., 2002). In contrast, there were no differences in thermotolerance between Brahman × Holstein embryos and Angus × Holstein embryos. These results indicate that either genes conferring thermotolerance are paternally imprinted (only the maternal allele being expressed) or that thermotolerance in embryos depends upon some genetically-controlled factor produced in the oocyte.

How important are genes conferring cellular thermotolerance for the overall adaptation of *B. indicus* to hot climates? One experiment that could address this question would be to test whether embryonic survival after transfer into heat-stressed recipients was dependent on embryonic genotype. Data by Turner (1982) would suggest that regulation of body temperature is the most critical factor for genetic differences in reproductive function during heat stress since the depression in fertility per unit increase in body temperature was the same for *B. indicus* × *B. taurus* crossbred cows as for Hereford × Shorthorn cows.

4. Exploitation of *B. indicus* genotypes to increase thermotolerance in cattle

As stated earlier, zebu cattle exposed to heat stress experience less severe alterations in feed intake, growth rate, milk yield, and reproduction than do cattle from *B. taurus* breeds

that are not adapted to warm climates (Kibler and Brody, 1951; O'Bannon et al., 1955; Cartwright, 1955; Johnston et al., 1958, 1963; Allen et al., 1963; Johnson, 1965; Skinner and Louw, 1966; Seif et al., 1979; Rocha et al., 1998). In addition to being thermotolerant, zebu cattle are tick resistant (Rechav, 1987) and efficient at digesting poor quality forages (Hunter and Siebert, 1985). Not surprisingly, much use has been made of zebu genotypes to develop cattle for beef and dairy production in the tropics and semi-tropics. There are, however, other genetic characteristics of zebu cattle that limit their usefulness as beef and dairy animals including poor meat tenderness (Wheeler et al., 2001), low milk yields and lactation persistency (Madalena et al., 1990; Thorpe et al., 1994; McDowell et al., 1996; Murugaiyah et al., 2001), a long prepubertal period (Rodrigues et al., 2002), short duration of estrus (Plasse et al., 1970; Rae et al., 1999), and poor temperament (Hammond et al., 1996; Voisinet et al., 1997). In dairy cattle systems, utilization of zebu crossbreds in hot climates becomes more beneficial relative to purebred European breeds as the overall level of feed resources and other inputs decline (Madalena et al., 1990; McGlothen et al., 1995).

An alternative scheme to crossbreeding for utilizing the zebu genotype for livestock production in hot climates is to incorporate those zebu genes that confer thermotolerance into European breeds while avoiding undesirable genes. An example of this strategy using conventional breeding approaches comes from the Senepol and Carora breeds which are *B. taurus* in which criollo genotypes have been incorporated. Olson et al. (2003) have identified a phenotype characterized by development of a very short, sleek hair coat that is inherited as if controlled by a single dominant gene. Cattle inheriting the *slick hair* gene are better able to regulate body temperature and, for Carora, have higher milk yields (Olson et al., 2003). Identification of specific gene loci conferring thermotolerance in zebu cattle could be followed by crossbreeding and selection for the favorable allele using phenotypic traits or molecular markers.

Efforts have been made to identify specific loci in zebu crossbreds that affect carcass and growth traits (Casas et al., 2003) but no effort has been described for identifying genetic markers for thermotolerance. Care must be taken in doing so to avoid inadvertent selection of genes for reduced production (since genes causing low feed intake and low milk yield would increase thermotolerance). This problem could be avoided by identifying candidate genes known to be involved in thermotolerance. An analogy can be made to efforts to select for growth loci based on the growth hormone 1 gene (Taylor et al., 1998).

The advent of molecular genetics, marker assisted selection, and transgenics makes the strategies outlined in the previous paragraph technically feasible. However, realization of the promise these technologies offer awaits intensive research into the molecular basis for thermotolerance in cattle. Almost nothing is known about specific genes controlling heat resistance in zebu cattle and, indeed, our understanding of the physiological basis for thermotolerance in these cattle is still incomplete. As is apparent from this review, much of the research into the physiological mechanisms responsible for thermotolerance in zebu cattle was conducted before 1970. These early researchers were frequently audacious in their approach and their work often remains unsurpassed to this day (see Bianca (1965) for a thorough review of the early literature). In addition, however, these studies frequently involved limited numbers of animals and there was not access to the range of methodologies available today. There is a compelling need to use modern methods to further define the physiological and cellular basis for thermotolerance in zebu cattle and to identify the genes

responsible. Once this is accomplished, the complete armamentarium of modern genetics can be brought to bear to exploit the zebu genome for livestock production.

Acknowledgements

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