



Review Article – Agriculture

The role of phenotypic and genetic basis of livestock selection for climate change adaptation and mitigation: A review

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Abstract

Livestock are not only suffering from climate change but also contribute to climate change through the direct and indirect release of greenhouse gases (CH₄, N₂O, and CO₂). Characterization, identification, and conservation of heat tolerant livestock breeds are the basics for the future challenging climate. Properties of the skin, hair, coat color, coat type, sweating, respiration capacity, tissue insulation, surface area relative to body weight, endocrinological profiles, and metabolic heat production are important factors involved in heat tolerance. Selection based on these phenotypic characteristics could have an indispensable contribution to climate change adaptation and mitigation. Molecular information is used to know the candidate genes for heat tolerance, their action, specific function and location on chromosomes and thereby important for modification of gene and selection of heat tolerant and feed efficient animals. Marker-assisted selection and proteomics may also be valuable in selection for secondary traits linked to adaptation, such as the genes for high levels of blood urea and ruminal ammonia in certain genotypes, associated with adaptation to low-quality C4 grasses. Scientific research results demonstrated that heat tolerance is a heritable trait and there is variation between/within livestock breeds, thereby this variation and heritability of the trait open the window for selection of heat-tolerant animals. Therefore, combining genomic selection using genome-wide DNA markers that predict tolerance to heat stress and phenotypic selection could accelerate breeding of highly productive and heat tolerant livestock breeds. This, in turn, calls for further research on molecular characterization & identification of indigenous breeds and on the identification of genes/genomic regions associated with thermoregulation, feeding and production efficiency in order to develop suitable adaptive and mitigation strategies.

Keywords: Climate change, genomic selection, introgression, livestock, phenotype selection

Introduction

Climate change is arguably the most important environmental issue of our time. With severe and widespread destructive effects, warming of the planet threatens ecological systems, peoples' livelihoods, and species survival (IPCC, 2014). Animal agriculture is an important source of greenhouse gas (GHG) emissions and has been implicated as a serious contributor to climate change (Gerber *et al.*, 2013). This makes livestock unique in the sense that they not only suffer from climate change but

reproductive, production and health traits. Because of global warming, livestock in developing countries will have to adapt to higher ambient temperatures, a lower nutritional value of grasses in some cases, and expansion of the occurrence of parasites and diseases, especially ticks and tick-borne diseases (Scholtz *et al.*, 2011). With such challenges, proper trait definition and matching genotype with production environment will become crucial. The selection of animals and genotypes that are better adapted to the production system, including heat stress, is possible and should be pursued to ensure sustainable production in these innovative breeding strategies.

continued uncontrolled release of GHG thus has a twofold implication for the livestock industry, and consequently food security (Scholtz *et al.*, 2013). Moreover, directly or indirectly climate change has impacts of on AnGR through catastrophic events, disease epidemics, productivity losses, physiological stress, water availability, agro-ecological changes (fodder quality and quantity, host-pathogen interactions and GHG reduction) and resource price/availability (feed production) (Hoffmann, 2010).

Therefore, an improved understanding of the production environmental adaptation of livestock is important which is a complex trait and difficult to measure. Fortunately, several proxy indicators for adaptation are available such as

Livestock industries have a responsibility to reduce the release of GHG (i.e. the carbon footprint) and water use (i.e. the water footprint) of livestock production. An effective way of withdrawing the carbon and water footprints from livestock is to reduce livestock numbers and increase productivity per animal. Increased production generates less GHG emission per unit of livestock product (Capper, 2013). Production efficiency can be improved through breeding and genetic improvement. Genetic improvement of livestock is a function of natural selection and human intervention. Whereas fitness and adaptability have shaped the course of natural selection - livestock keepers and animal breeders have brought improvement through the application of their

Table 1. Global GHG emission from each livestock species in 1961 & 2016 (in gigagrams)

Sources	GHG	Year	DC	NDC	Goat	Sheep	Horse	Camel	Mule	Swine	Broiler	Layer
Enteric fermentation	CH4	1961	15963.9	33445.1	1743.6	6477.5	1118.9	594.6	104.8	52.3	-	-
	CH4	2016	18592.3	53317.5	5014.1	6563.8	1062.9	1309	97.7	112.3	-	-
	CO2	1961	335241.2	702346.5	36616.3	136028	23497	12487	2200	1098.4	-	-
Manure management	CO2	2016	390437.9	1119668.5	105295.1	137840	22320	27488	2052	2359.1	-	-
	CH4	1961	2652.9	1546.1	55.7	178.2	94.9	28	8.7	272.4	36.6	269.3
	CH4	2016	2137.6	1884.5	171.3	187	90.7	66.3	8.2	487.3	273.7	383.2
	CO2	1961	84046.1	73479.2	1577.2	7185.2	2249.1	611	193.5	7930.2	2059.3	7755
	CO2	2016	63005.5	93081.9	4747.7	7322.1	2122.7	1426.3	182.2	13751	13726	14116
	N2O	1961	91.4	132.3	1.3	11.1	0.8	0.1	0	7.1	4.2	6.8
N2O	2016	58.4	172.6	3.7	10.9	0.7	0.1	0	11.3	25.7	19.6	

DC: Dairy cattle; NDC: non dairy cattle. (Source: FAOSTAT, 2016)

wisdom, science, and technologies. The diversity and variability in the phenotype and genotype of livestock offers the opportunity for genetic improvement. Therefore, ideal breeding strategies and genetic improvement method can improve the productive efficiency and thereby reduce the GHG emission from the livestock sector. Thus, the main objective of this paper was to quantify the role of phenotypic and genetic basis of selection for climate change adaptation and mitigation through an intensive literature review.

The links between livestock production and climate change

The contribution of livestock for climate change

Livestock contributes both directly and indirectly to climate change. Enteric fermentation and manure associated emissions are direct, while production and transport of feed (including the fossil fuels used in manufacturing chemical fertilizers) and land use changes (such as conversion of forest to pasture and cropland) contribute indirectly (Hristov *et al.*, 2013). When a forest is cleared for pasture and feed crops, large amounts of carbon stored in vegetation and soil are also released into the atmosphere. In contrast, when good management practices are implemented on degraded land, pasture and cropland can turn into net carbon stores, sequestering carbon from the atmosphere. About 44% of the emissions generated by livestock are CH₄, which is released during enteric fermentation (eructation in ruminants) and emitted from manure decomposition; 27% are in the form of CO₂ emitted during the production and transport of animal products and feed, and 29% are N₂O attributable to manure and fertilizer (Gerber *et al.*, 2013).

Digestion of feed components by the microbiota (bacteria, protozoa, fungi) results in the production of volatile fatty acids. These acids, mainly acetate, propionate, and butyrate are used by the animal as a source of energy. During the process, gases are also formed and their production eliminated mainly through eructation. CO₂ and H₂ are using to form CH₄, and thus reducing the metabolic H₂ produced during microbial metabolism (Cassandro *et al.*, 2013; McAllister and Newbold, 2008).

In addition to enteric (animal-derived) CH₄, excreta are another source of CH₄, especially when stored anaerobically (Klevenhusen *et al.*, 2011). Methane generated from manure from ruminant and nonruminant livestock contributes 2% and 0.4% of global CH₄ and GHG emissions, respectively. Manure emissions are relatively high in areas where manure from the dairy sector is managed in liquid systems that produce greater quantities of CH₄ emissions (Gerber *et al.*, 2013). During manure storage, CH₄ is generated through a

reaction similar to that of enteric fermentation. Cellulose in the manure is degraded by microbes, with products of this process serving as substrates for methanogenesis (Chianese *et al.*, 2009a).

Note that enteric methane produced by ruminants is a loss of feed energy from the diet and represents an inefficient utilization of the feed (Chagunda *et al.*, 2009). In addition to environmental implications, ruminant methanogenesis represents a loss of 2% to 12% of the gross energy intake (Benchaar and Greathead, 2011; Pinares-Patiño *et al.*, 2007). However, it was found that small amounts of CH₄ are formed also from birds. Methanobrevibacter-related phylotypes have been found to be the most prevalent methanogens in the foregut and in the hindgut of the chicken of the hoatzin (*Ophistocomus hoatzin*). Therefore, proper management of manure, increasing feeding efficiency, increasing productivity and decreasing number of livestock might be the mitigation measures for climate change associated with livestock.

Impact of Climate Change on Livestock Production

Growth and meat production

Growth is defined as the irreversible positive changes in the measured dimensions of the body. Body growth is affected by factors such as nutrients, hormones, enzymes, and temperature. The significant influence of thermal stress on growth gain could be directly attributed to lower feed intake associated with reduced anabolic activity (Marai *et al.*, 2007). Further, thermal stress causes a reduction in the body condition score (BCS) due to negative energy balance. Factors such as greater maintenance requirements during hot weather, poor appetite and low-quality forages during summer months contribute to the slower growth and reduced body size (West, 2003). This reducing body weights can be partly explained by the lower dry matter intake of these animals during hotter parts of the day. In addition, elevated production of catecholamines and glucocorticoids during thermal stress condition may lead to increased tissue catabolism which occurs principally in fat depots and/or lean body mass of animals. Studies conducted in heat-stressed animals showed redistributed blood flow to the body surfaces (Ooue *et al.*, 2007; Leon, 2008) to facilitate heat dissipation to the surrounding environment which may also lead to earliest gastrointestinal ischaemia and hypoxia in them (Hinnebusch *et al.*, 2002). This leads to improper food assimilation and thereby results in subnormal growth.

Climate change is observed to have significant effects on the meat industry by altering both meat quality and safety. Heat stress influences meat quality mainly in two ways.

Exposure of the animals to hotter environments directly affects the organ and muscle metabolism, for example, increased ultimate pH and dehydration rate are seen in heat-stressed livestock, and the effects appeared to be persisting even after slaughter. In addition to the former effects, revised management practices during stressed periods further modify the meat quality of livestock and poultry indirectly. Adoptions of various management strategies like selection of thermotolerant sheep breed for production purposes may lead to altered mutton characteristics such as increased toughness, less juiciness, and less marbling. Additionally, changes in ambient temperature may also lead to altered microbial burdens on carcass and meat, especially in animals that carry more enteric pathogens. Apart from slaughter and post-slaughter changes, climate change can also affect pre-slaughter parameters by increasing the chances of transport mortality (Gregory, 2010).

Reproduction

Reproduction is considered as pleasure for farm animals, and at the same time, it is an energy-consuming process. Hence, climate change-induced negative energy balance in farm animals during hotter season significantly hampers their reproductive efficiency. The probable harmful consequences of thermal stress established in other species can be extrapolated to reproduction in sheep that includes the following: in females, the oestrus incidences, follicular dynamics, embryo development, fertilization, conception rate, lambing rate and birth weight of lambs were found to be adversely affected by heat stress (Sejian *et al.*, 2011) while in males, the sexual behavioural pattern, scrotal and testicular measurements, seminal attributes, process of spermatogenesis and spermiogenesis and ability of sperm to fertilize the ovum were affected by heat stress (Wolfenson *et al.*, 2000). The elevation of temperature had an adverse influence on mating, fertility and overall reproductive physiology of farm animals.

Milk production

Heat stress-induced reduction in nutrient intake is a major cause of reduced production and accounts for approximately 50% of the decrease in milk yield. The physiological responses to heat stress in dairy cattle include altered hormonal status, reduction in rumination and nutrient absorption, suboptimal immune function, and increased maintenance requirements resulting in a net decrease in nutrient/energy available for growth, reproduction, and lactation (Baumgard and Rhoads, 2013). According to Opio *et al.* (2013), the world emission for milk production is similar for sheep and goats with little higher values of CO₂ eq. emitted per kg for sheep than goats. The global average of the carbon footprint for milk production for small ruminants is more than double than large ruminants. Sheep milk from animals exposed to high temperatures resulted in higher neutrophil counts and also an increase of lipolytic and proteolytic enzymes (Sevi and Caroprese, 2012). High ambient temperature may also result in plasma mineral imbalance, due to a reduction in Na, K, Ca, and P and increase in Cl concentrations (Caroprese *et al.*, 2012).

Wool yield and quality

Climate change may have substantial effects on the sheep livestock, thus on wool, directly and indirectly. Extreme weather, drought, floods, rise in temperature, and

water availability can directly impact the sheep livestock. The agroecological changes, fodder quantity and quality, and disease epidemic may affect indirectly (Thornton, 2010). The declining number of sheep and reduction in average fleece weight due to pasture conditions may cause a further drop in wool production (Berry, 2015). The wool yield will depend on climate and pasture variables for particular regions. Wool production is a function of pasture growth and animal genetics. The wool-producing ability of a lamb depends on secondary follicle generation which is related to feed intake during gestation of the ewe. The low feed intake can cause follicle impairment in lambs (Harle *et al.*, 2007). High cost of fertilizers and reduced pasture production will invariably reduce feed quality and quantity to sheep. In addition, high heat stress on sheep in the tropical and subtropical regions due to rise in temperature may lower the wool yield. Wool-producing breeds are being replaced by dual-purpose sheep breeds. This may hamper the wool production. Wool-producing breeds are at risk due to low-profit margins and therefore face the risk of becoming extinct. It is a threat to biodiversity and may further lead to intangible adverse impact on climate change.

Fiber diameter, fiber diameter variation, staple length, staple strength, and amount of impurities are some of the important traits which determine its performance during subsequent processing stages. All these important traits are likely to be influenced by the effect of climate change. The fiber diameter may shift from finer to coarser quality with the rise in temperature and reduction in rainfall. In the climatic variability, it would be a challenge to produce and sustain fine quality wool for apparels, whereas, the coarse quality wool can be more resistant to climate change (Harle *et al.*, 2007). The raw wool in high rainfall region is likely to have high vegetable matter content. Low rainfall region may also lead to accumulation of high amount of dirt and dust in the raw wool. In both cases, energy-intensive cleaning operations will add cost and also deteriorate fiber traits, like length and staple strength, affecting the quality of the final product (Harle *et al.*, 2007). However, this would reduce income from wool since fine quality wool always yields good price. The influences of climate change on wool quality traits thereby reduce the income of smallholders.

Characterizing the potentials of genetic resources in coping with climate change

Many breeds in the developing and underdeveloped countries are yet to be characterized and possess worth information with regard to traits of importance. There are several breeds which are important for disease resistance traits, feed efficiency traits, heat tolerance traits, etc., and all these breeds must be characterized for their probable future use (FAO, 2015). When animals are exposed to heat stress the biological functions affected include depression in feed intake and utilization, disturbances in the metabolism of water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites (Marai *et al.*, 2007), resulting in the impairment of production and reproduction performances. The effect is aggravated when heat stress is accompanied by high humidity. Tropical breeds tend to have better heat tolerance than breeds from temperate zones. A range of factors are involved, including properties of the skin and hair, sweating and respiration capacity, tissue insulation, surface area relative to body weight or lung size, endocrinological profiles and metabolic heat production. As

milk yield in dairy cattle has risen, and growth rates and leanness in pigs and poultry have increased, the animals' metabolic heat production has increased and their capacity to tolerate high temperatures has declined (Zumbach *et al.*, 2008). Turner (1980) extensively reviewed the genetic and biological aspects of zebu adaptability and attributed their unique suiting to hot climates to coat, hide, skin, hematological characteristics, form, growth, and physiological aspects which are unique genetic attributes of zebu compared to *Bos taurus* cattle. Zebu cattle are smooth coated, have primary hair follicles, have better-developed sweat and sebaceous glands than *B. taurus* cattle and can lose more moisture by evaporation and hence have the ability to maintain a thermal equilibrium that is a necessary factor for normal function and performance (Turner, 1980). McManus *et al.* (2009b), working with five naturalized and two exotic cattle breeds in Brazil, found that the Junqueira and Nellore breeds were the most adapted to the climatic condition while Mocho Nacional and Holstein breeds were least adapted. Finocchiaro *et al.* (2005) reported the genetic correlation between the general additive effect of milk production and the additive effect of heat tolerance to be negative ($r = -0.8$) during all periods considered indicating that selection for increased milk production will reduce heat tolerance.

According to ILRI (2007) report, Sheko breed which is found in Ethiopia has been recognized as one of Africa's "Big Five" vintage cows having great potential to form the genetic backbone for future survival. Dadi *et al.* (2009) had also explained characters related to disease resistance and adaptation to extreme environments of breeds could prove fundamental to food security for the present and future human generations. Sheko cattle is one of the trypano-tolerant cattle breeds in Africa which are able to thrive in the trypanosomiasis infested areas of South and South-west parts of Ethiopia, where trypanosomiasis coverage exceeds 180,000 to 200,000 km² of agriculturally suitable land.

Conservation of local genetic resources

Increasing productivity and efficiency will be fundamental in a manner that maintains genetic diversity. Despite the potentials of diversified genetic resource, the huge loss of livestock genetic diversity in developing countries will seriously undermine the efforts towards achieving food security and poverty reduction (Zerabruk *et al.*, 2007a) *viz-a-viz* the long-term effect on global biodiversity. More than 31% of the world cattle breeds are currently at risk and already extinct (FAO, 2009a). Especially, the situation is very serious in the developing world where rapid changes in production systems are leading to a replacement of the breeds or at best cross-breeding (Zewdu, 2010).

Local breeds usually possess an innate ability to adapt to the local climatic conditions, various stressors and available feed resources. However, in developing countries, advancement in animal breeding and agricultural activities which could have otherwise helped to augment the adaptation process is at a slow pace. The adaptation strategies take into account not only the ability of the animal to tolerate the climatic stressors but also their survivability, growth and reproductive performance during periods of feed scarcity, parasite load and disease occurrence (Hoffmann, 2008).

Conserving local breeds which are adaptive to the local environment are critically important. It is strongly believed

that to adapt the production systems to radically changing conditions, local breeds offer diversity which is the only base for future selection and adaptation as does plant genetic diversity (ILRI, 2007). For instance, both Boran and Begait are drought tolerant and withstand water thirst. Boran cattle can stay two to three days without thirst (Nigatu *et al.*, 2002). The genes that Boran cattle carry are mainly the result of a long-term natural selection under harsh environmental conditions. They have developed adaptive traits of crucial importance for their survival. Zerabruk *et al.* (2007b) indicated that Begait cattle breed is well adaptive to arid and semi-arid conditions whereas Fogera cattle adapt to survive in flooded and swampy areas for several months. Conserving and enhancing the productivity of these types of indigenous breeds is crucial to oppose future climate change effect. In addition to conservation, within breed phenotype and genome-based selection and proper management could improve the productivity of livestock.

Developing heat tolerant breeds

There are clear genetic differences in resistance to heat stress, with tropically adapted breeds experiencing lower body temperatures during heat stress than nonadapted breeds. Even in nonadapted breeds, it is probably possible to perform genetic selection for resistance to heat stress (Sahoo *et al.*, 2013; Sejian *et al.*, 2017). There are also specific genes that could be selected which confer increased thermoregulatory ability. It may be possible to identify genes that control cellular resistance to elevated temperature. The superior fertility of tropically-adapted breeds during heat stress is a function in large part of the enhanced ability of animals from these breeds to regulate body temperature in response to heat stress. However, certain tropically-adapted breeds are also more resistant to an elevated temperature at the cellular level. Identification of the genes responsible for enhanced cellular resistance to heat shock may allow these genes to be transferred into thermally-sensitive breeds through conventional or transgenic breeding techniques to produce an animal whose oocytes and embryos have increased resistance to elevated temperature (Sahoo *et al.*, 2013). Gene knockout technology will also allow better delineation of cellular metabolic mechanism required for acclimatization to thermal stress in sheep and goats. By knowing the various genes responsible for thermotolerance we can change the genetic structure of animal and drift towards superior thermo-tolerant ability (Collier *et al.*, 2008).

Initially, breeding schemes to improve adaptation should be based on the selection of appropriate breeds that are adapted to the local environmental conditions, before undertaking within-breed selection programs to improve resistance (Burrow, 2006; Bishop, 2012) or involving the breed in an introgression scheme (crossbreeding). Based on recent reviews of the literature, genetic tolerance/resistance to environmental stressors usually follows polygenic patterns of inheritance, as do production traits (Bishop, 2012; Burrow and Henshall, 2014). When population-wide genomic testing becomes cost-effective in the near future, tests for tolerance traits will need to be fully integrated into quantitative genetic evaluation programs.

Practically, to genetically improve tolerance traits through breeding practices, the traits must be under direct or indirect genetic control that can be detected by genetic parameters. Bishop and Morris (2007) reported that

heritability for FEC differed in both sheep and goats, depending on the age of measurement, with FEC tends to be less heritable in kids and does. Bishop's (2012) review also indicated that PCV was heritable in sheep and goats and that Famacha scores (an indicator of anemia in the eyelid) were heritable in sheep. Additionally, the concentrations of various antibodies, eosinophils, pepsinogen, and fructosamine were moderate to highly heritable and often strongly correlated with FEC. It was therefore concluded that breeding to improve resistance utilizing these traits in livestock species is possible. Traits of tolerance to other abiotic stresses as measured by changes in rectal temperature have been reported in young calves with a moderate value of 0.19 (Morris *et al* 2012) and in dairy cattle (Dikmen *et al.*, 2012) who reported an average value of 0.17, indicating the possibility of genetic improvement of such traits is highly associated with tolerance/adaptation performance of several stressors. Efforts to assess the genetic parameters for adaptation measures (thermal, respiratory, and metabolic) require more research efforts.

Selection for robustness would likely require the development of an index involving multiple traits. Aboul-Naga *et al.* (2010) suggested a useful index that relied on changes in some biological parameters such as rectal temperature, respiration rate, tidal volume, minute-ventilation volume, and heat production due to both heat and exercise stresses to assess the animal tolerance to grazing stress in the hot, arid desert. Heritability of some of such traits and genetic markers associated with tolerance has been estimated (Elbeltagy *et al.*, 2016). The variation between breeds and heritability of heat tolerance related traits demonstrates a bright future for the development of breeds through continues selection, crossbreeding and genetic introgression. This could be conducted between tropical and temperate breeds or within tropical breeds based on the variation for heat tolerance and feed efficiency.

Developing suitable breeding program

Development of appropriate breeding program (pedigree and performance recording, breeding objective identification and intervention through selection of the best and culling of unfitted for desired/predetermined breeding goal) is the basis for effective livestock breeding: increases the genetic gain, feed efficiency and reduce greenhouse gas emission per animal.

Record keeping

The goal of livestock recording schemes is usually to provide farmers with information about individual animals for management and breeding purposes (Kosgey *et al.*, 2011). Although livestock identification, pedigree and performance recording is an important ingredient in adaptation to climate change, it has been given little attention by both the farmers and policymakers in developing countries (Okeno and Wasike, 2016). This could be due to lack of scientific information to demonstrate to farmers and policy makers the potential benefits of livestock recording in relation to increased productivity and adaptation to climate change. It is believed that with intensive pedigree and performance recording the local breeds could realize higher response to selection for both productive and adaptability traits than imported breeds.

Identifying breeding objectives

Breeding objective is defined as the reason (s) for which animals are specifically bred for, it assumes that the farmers have made a deliberate choice to genetically improve the next generation of animals in terms of their performance in relation to their parent generations (Godadaw *et al.*, 2014). The breeding objective in any livestock species is to increase profit by improving production efficiency (Charfeddine, 2000). Identifying the selection criteria, which are the traits that should be used in selecting animals (Mokolobate *et al.*, 2013). Traits in the selection criteria should be correlated with the traits in the breeding objective, easily measurable and heritable. Until now, most measurements to improve production in developing countries, and many other parts of the world, are per individual (milk production, fibre production, weaning weight, calving interval, growth rate, etc.). Selection for these traits will increase production, but not necessarily productivity or efficiency of production. Measurements are thus required that express performance per constant (standardized) unit. Selection for productivity and efficiency, for instance, will have a permanent mitigating effect on the production of GHGs, as higher productivity will lead to higher gross efficiency as a result of diluting the maintenance cost of animals (Wall *et al.*, 2008; Scholtz *et al.*, 2011). Proper trait definition is therefore important for achieving the desired breeding goal (improve trait of interest) and thereby reducing GHG emission by enhancing productivity/animal and reducing unproductive livestock numbers.

Selection strategies

Having diverse AnGR will allow for more opportunities to match breeds to a changing climate or to replace populations hit by severe climatic events such as droughts and floods. Within breed, broad genetic diversity will clearly allow for greater opportunities for selection for adaptation, but there is evidence from wild populations that increased genetic diversity is also selectively advantageous on the individual level (Fourcada and Hoffman, 2014).

Selection for phenotypic characteristics

Maintaining diversity in genetic resources and approaches is the basic concept of resilience. A diversity of farming practices allows livestock keepers to cope with differences in local environments. The traits of inherent resilient and adaptive capacity against heat stress are long legs, short hair coat, higher sweating rate, large surface area, body conformation, higher capacity for maintenance of heat balance, lower metabolic rate, higher feed efficiency, higher tolerance to dehydration and adipose tissue depots, and capacity to alter the hormone and biochemical profiles to adapt to a particular environment (Sejian *et al.*, 2017).

Selection for coat color, coat type, and hair characteristics

During periods of elevated temperature, evaporative heat loss is an important mode of heat loss (Collier *et al.*, 2008). While external factors will have a significant effect on evaporative heat loss including wind speed, ambient temperature, and relative humidity, the phenotype will also have a role. Phenotypes that are important include coat characteristics such as density, thickness, hair length, and colour. Similarly, skin properties such as sweat gland density and function, skin colour and regulation of epidermal

vascular supply have been implicated (Olson *et al.*, 2006). For example, Zebu cattle have a light-colored hair coat that is sleek and shiny while European type cattle have a denser, wooly coat typically darker in color. The sleek and shiny hair coats of the Zebu cattle reflect a greater proportion of incident solar radiation than those of *Bos taurus*. The coats of *Bos taurus* cattle reduce heat flow by means of conduction and convection and increase the effects of heat stress.

SLICK is a dominantly inherited phenotype of tropically adapted *Bos taurus* cattle that is characterized by very short, smooth and sleek hair coat, naturally found in Senepol, Carora, Criollo Limonero and Romosinuano breeds (Brenneman *et al.*, 2007; Landaeta-Hernández *et al.*, 2010). This naturally selected trait is considered a very interesting feature for breeders and researchers due to its significant role in thermo-tolerance, as well as potential association with higher productivity and disease resistance (O'Brien *et al.*, 2010; Scharf *et al.*, 2010; O'Neill *et al.*, 2010). As a result, selective breeding for tropically adapted *Bos taurus* with characteristics such as SLICK could contribute to improved thermo-tolerance, especially in the dairy industry. Hence, a number of studies are underway to determine the gene or genes responsible for heat tolerance in SLICK cattle in order to introduce it into the dairy industry in hot environments (Huson *et al.*, 2014; Flori *et al.*, 2012).

Coat color is a qualitative trait and an indicator of adaptability to heat stress (Fadare *et al.*, 2013; McManus *et al.*, 2011). Coat color is an important trait of biological, economic, and social significance. The genetic cause of domestic white and black sheep involves a tandem duplication affecting the ovine *agouti signaling protein (ASIP)* gene and two other neighboring genes, *AHCY* and *ITCH* (Norris and Whan, 2008). Sheep coat color is regulated by a combination of copy number variation (in *ASIP*) and deregulated gene expression (*AHCY* and *ITCH* promoter). Norris and Whan (2008) identified some white sheep with up to four copies of the *ASIP* allele, while the black sheep have a non duplicated *agouti* allele and the silenced promoter that mutes its expression. Li *et al.* (2014), conducting a GWAS (genome-wide association study) of sheep coat colors using Illumina 50K SNP BeadChip in the Finn sheep population, identified 35 SNPs associated with all the coat colors in the studied breed, which cover genomic regions harboring the pigmentation genes including the previously identified *ASIP*, in addition to *TYRP1* and *MITF*. The signals detected around the *ASIP* gene were explained by differences in white versus nonwhite alleles.

Fadare *et al.* (2013) studied the effect of coat color on some physiological and blood parameters that are associated with climatic-stress-tolerance traits, including rectal temperature (RT), respiration rate (RR), pulse rate (PR), packed red cell volume (PCV), red blood cell count (RBC), white blood cell count (WBC), plasma sodium (Na^+) and potassium (K^+), in addition to a heat-stress index (HSI) in four sheep color categories of West African Dwarf sheep. Animals with a black coat showed the highest significant measures of RT, RR, PR, and HSI, respectively, followed by brown mouflon and brown with extensive white, while the Badger Face sheep had the lowest mean values. Coat color also had a significant effect on blood parameters (RBC, WBC, Na^+ and K^+). These results indicate that selection for white-coat-colored sheep to attenuate heat stress is desirable

in the hot humid tropics.

Selection for tail type

Adipose tissues accumulating in the tail are mobilized during periods of food scarcity and correspondingly tend to decrease in size during seasonal periods of weight loss. The uneven distribution of body fat in the tail has a thermoregulatory effect as an appendage favoring heat dissipation. The tall and slender “low-volume” types of bodies of fat-tailed sheep are also important adaptation characteristics to periods of heat stress in dry climates, and along with the longer legs, they are particularly suitable characteristics for walking long distances in search of pasture and water as in the nomadic lifestyles of herders in most arid dry regions of the world. Identification of genomic regions that have been associated with selection for phenotypic adaptation traits, such as tail fat deposition, is important and challenging areas of research in sheep genetics (Sejian *et al.*, 2017). Selective sweeps detected using the F_{ST} approach with the sheep HapMap – four thin- and three fat-tailed breed – data revealed that three of these regions were located on *Oar 5*, *Oar 7*, and *Oar X*. Increased homozygosity in these regions was detected favoring fat-tail breeds on *Oar 5* and *Oar X*, and was in favor of thin-tail breeds on *Oar 7*. This preliminary research reflected the association between fat-tail deposition genes and climatic-stress-tolerance performance. However, further investigations are still needed from this point.

In the same context of investigating the association of polymorphism of genes, regulating functions related to tolerance, reproduction, and production performance, with the fat-tail characteristics, Chelongar *et al.* (2014) studied the association of genetic polymorphisms within the insulin-like growth factor 1 (*IGF1*) and pituitary transcription factor 1 (*PIT1*) genes with fat-tail sheep. The association was tested in the Iranian Makooei sheep breed, using the conventional single-strand conformational polymorphism (SSCP). Results showed a significant statistical association between fat-tail measurements and genotypes of both genes. For the *PIT1*, the P3 genotype was found to be associated with superiority of both tail length and width ($P < 0.01$), while the P4 genotype showed an association with significant superiority of fat-tail thickness ($P < 0.01$). Meanwhile, the AA, AG conformational patterns of *IGF1* had a significant effect on fat-tail thickness ($P < 0.05$).

The association of SNP polymorphisms in both growth hormone (*GH*) and leptin (*LEP*) genes with fat-tail measurements (dimensions) in the same Makooei sheep breed was also investigated by Hajihosseini *et al.* (2015) using an SSCP (single-strand conformation polymorphism) denaturation approach in 100 ewes. The authors reported significant statistical associations between all fat-tail measurements studied and the *GH* and *LEP* genotypes. Individuals with the G4, L4 genotype of *GH* and *LEP* genes, respectively, had shorter tail length, less tail thickness, and width compared to individuals with other genotypes. The results also demonstrated that individuals with the G5 and L5 genotypes of *GH* and *LEP* genes were associated with a superiority of tail length and thickness, while individuals with the G2, L2 genotypes showed superiority in tail width. Therefore tail type could be an important trait for selection of heat tolerant sheep breeds.

Selection based on rectal temperature

According to Dikmen *et al.* (2012), the heritability of rectal temperature under heat stress conditions ranged from 0.13 to 0.17. This means that about 13-17% of the variation among cows in rectal temperature during heat stress is the result of variation in genetics. This value is relatively low compared to a trait like milk yield, where heritability is ~0.30 (Pritchard *et al.*, 2013), but it is high enough to allow selection for rectal temperature in order to select heat-tolerant cow directly if the rectal temperature is recorded. Data on variation in rectal temperature has been used to identify genetic markers that predict thermotolerance on the Illumina Bovine SNP50 BeadChip (Dikmen, Cole, Null and Hansen, unpublished). The Bovine SNP50 BeadChip is a genetic tool to estimate an animal's inheritance of specific mutations at 50,000 places on its chromosomes. With this information, obtained from a single sample of blood or hair, one can estimate genetic merit for milk yield, net merit, etc. Similarly, Hansen (2013) indicated that the use of genetic tests like the Bovine SNP50 BeadChip should make it possible to identify genetic markers that predict thermotolerance that is not related to milk yield. Selection for these markers could lead to an increase in thermotolerance without having adverse effects on milk yield. Methods of estimating genetic merit for heat-tolerance have been developed in Australia with clear results in sire selection. Hayes *et al.* (2009) evaluated records on daughters from 798 sires to determine the degree to which milk yield was depressed by heat stress. There was substantial variation

between bulls, as temperature humidity index goes from 60 to 90° F, milk yield in Sire 1 declines from about 40 lb/day to 28 lb/day. In contrast, there was no change in milk yield for daughters of Sire 2. A heat stress index based on these measurements could also be used to select bulls for thermotolerance. Therefore, rectal temperature can be used as direct selection criteria if the data is available used to identify genetic markers that predict thermotolerance.

Gene-based selection for climate change adaptation/mitigation

Gene-based techniques as applied to animal breeding and improvement include several marker-based technologies such as marker-assisted selection (MAS), gene-assisted selection (GAS), marker-assisted introgression (MAI) and genomic selection (GS). Since developments in quantitative trait loci (QTL) and genomic selection based on SNPs will enhance the detection and fine mapping of many genes and QTLs, it is foreseen that this will play a major role in selection for disease and parasite resistance or tolerance (Scholtz *et al.*, 2010). Marker-assisted selection and proteomics may also be valuable in selection for secondary traits linked to adaptation, such as the genes for high levels of blood urea (N) and ruminal ammonia (NH₃) in certain genotypes, associated with adaptation to low-quality C4 grasses. Traits associated with the measurement of individual feed intake, meat quality, milk composition, disease resistance/tolerance, etc., may be expensive and/or difficult to measure, which also makes them ideal candidates for marker-assisted selection.

Table 2. Candidate genes for cattle thermoregulation

Gene	Function	References
<i>STAC</i>	Response to heat	
<i>HSPH1, TRAP1</i>	Heat shock protein response	
<i>CCNG, TNRC6A, STAC, WRNIP1, MLH1, RIPK1, SMC6, GEM1</i>	Cellular response to stress	Howard <i>et al.</i> 2014
<i>ITGA9</i>	Respiration	
<i>NBEA</i>	Body weight and feed intake	
<i>CACNG3, CLCN4, PRKCB, TRPC5, KCNS3, SLC22A23, TRPC4</i>	Ion transport	
<i>NCAD</i>	Calcium ion and protein binding	Dikmen <i>et al.</i> 2012
<i>FGD3, G2E3, RASAI, CSTB, DAPK1, MLH1, RIPK1, SERPINB9, HMGB1</i>	Apoptosis	Howard <i>et al.</i> 2014
<i>FGF4</i>	Cell signaling and Apoptosis	Hayes <i>et al.</i> 2009
<i>DIO2, SLCO1C1</i>	Thyroid hormone regulation	Dikmen <i>et al.</i> 2012; Howard <i>et al.</i> 2014

Candidate genes for thermoregulation

A candidate gene is a gene supposed to be responsible for a considerable amount of the genetic variation of a trait. The candidate gene approach is based on the search for DNA polymorphism in genes that are expected, from knowledge of their physiological role for their position along the genome or for their level of expression, to have an influence on the target trait. Therefore, rather than searching for a relative gene randomly through the whole genome, it is desirable to focus on genes, which may already be suspected to have a role in the expression of the trait, that we want to investigate.

Genomic selection

The implementation of genomic selection technology

involves genotyping selection candidates to predict breeding values, which can be performed in the absence of phenotypic records. With the availability of high-density marker-maps and cost-effective genotyping, GS methods may provide faster genetic gain than can be achieved by traditional selection methods. Functional genomics research is providing new knowledge about the impact of heat stress on livestock production and reproduction. Using functional genomics to identify genes that are up- or down-regulated during a stressful event can lead to the identification of animals that are genetically superior for coping with stress and toward the creation of therapeutic drugs and treatments that target affected genes (Collier *et al.*, 2012). Further, gene knockout models in single cells also allow for better delineation of the cellular metabolic machinery required to acclimate to thermal stress. With the development of

molecular biotechnologies, new opportunities are available to characterize gene expression and identify key cellular responses to heat stress. These new tools enable to improve the accuracy and the efficiency of selection for heat tolerance. Epigenetic regulation of gene expression and thermal imprinting of the genome could also be an efficient method to improve thermal tolerance.

Genetic selection of animals that consume less feed or produce less CH₄ per unit of feed is a management strategy that may be used to reduce enteric CH₄ emissions. Pinares-Patino *et al.* (2007) established that there are differences between individual animals in the quantity of CH₄ they emit per unit of dry matter intake. Animal effects on fermentation could be via the saliva, feed processing (e.g., comminution), or flow rate through the rumen. It is possible that the animal's impact on fermentation is genetically determined and if this is the case it may be possible to obtain markers that can be used to select low methane emitters. The inclusion of information from DNA analysis in the genetic evaluations or estimation of breeding values in dairy cattle will have a great impact in dairy cattle breeding as it will increase the accuracies of breeding values of young bulls and decrease the generation interval (McDonald and Rickards, 2013). Strategies that utilizes EBVs derived from DNA information (genomic EBVs), together with conventional mixed model methodology, may speed up the process of breeding animals that are adapted to the newly created environments, as a result of climate change.

Increases in the productivity of swine, largely achieved through genetic selection, have been cited as climate change mitigation progress (Hristov *et al.*, 2013). For example, a 2013 FAO report cited data provided by the US National Pork Board. Between 1959 and 2009, there was a 29% increase in the number of hogs marketed in the United States, yet the size of the breeding herd has been reduced by 39%. This is due in part to the steady increase in litter size from 7.10 in 1974 to 9.97 piglets in 2011 and the concomitant change in the amount of pork produced from a single breeding animal from 775 to 1828 kg. Feed efficiency also increased by 33%. This has reduced the carbon footprint per 454 kg of hot-dressed carcass weight produced by 35% (Hristov *et al.*, 2013). Swine and poultry produce relatively small amounts of enteric CH₄, but their manure can be a significant source of GHG production. Therefore, maintaining or improving feed conversion efficiency in these species, and subsequently reducing the volume of manure produced for a given level of output, is considered a major strategy for mitigating CH₄ and N₂O (Hristov *et al.*, 2013). Therefore, genetic selection has indispensable role to select heat tolerant, feed-efficient and productive animals in order to cope the future climate change.

Marker-assisted introgression

Genetic introgression is the movement of a gene or gene flow from one species into the gene pool of another by the repeated backcrossing of an interspecific hybrid with one of its parent species (<https://en.wikipedia.org/wiki/Introgression>). Because of long generation intervals, lower reproductive rates and greater rearing costs in large livestock, introgression is only feasible in livestock for genes of large effect (Rajesh *et al.*, 2015). By using marker technology in breeding, the transfer of genes that control desired phenotypes between breeds is

possible. If the genes controlling resistance to the specific disease were identified, it would be possible to transfer them from the indigenous breed into the improved breed, thus, producing stock that has an increased production potential and is resistant to endemic disease. The introgression of disease resistance genes into the improved breeds would be achieved initially by crossing the indigenous and improved breeds. The first generation crossbred animals would then be backcrossed to the improved breeds and the animals genotyped for the genes involved in the disease resistance. Animals carrying the favorable alleles would be selected for breeding and backcrossed again to the improved breed (Rajesh *et al.*, 2015). By repeated backcrossing and selective breeding from the animals carrying the favorable disease resistance alleles, it is possible to recover the majority of the genome from the improved breed while maintaining the disease resistance that originated from the indigenous breed.

A dominant “slick” gene first described in Senepol breed of beef cattle in the Virgin Islands, that causes very short hair growth was introduced into Holsteins cows in Florida, and the resulting offspring were better able to regulate their body temperature during heat stress than cows with normal hair (Dikmen *et al.*, 2008). Therefore, through the use of molecular marker technology, it is possible to transfer heat resistant gene from indigenous breeds to temperate breeds so as to improve simultaneously the productivity, diseases and heat tolerance.

Considering G x E interaction

The single most effective GHG mitigation strategy in many regions of the world is to increase animal productivity (Hristov *et al.*, 2013). Raising imported animals selected for production traits, instead of traditional breeds is part of that strategy. However, the FAO also cautions that while achieving the genetic potential of highly productive breeds is important, these animals should not be imported into environments where climate or management limitations would prevent the animals from achieving this potential. In new regions or countries, animals from genetic lines with high production potential may actually perform worse than native breeds or crossbreeds, especially compared to those well-adapted to local disease and climatic conditions (Hristov *et al.*, 2013). Some regions have seasonal fluctuations in feed quality and nutrient management, and, as high genetic merit breeds have exacting nutritional requirements, they do not always thrive as expected.

In Africa, resistance to trypanosomiasis is a factor that limits the geographical distribution of cattle breeds. Indigenous taurine (humpless) breeds of cattle including the N'Dama and West African Shorthorn are genetically trypanotolerant (Murray *et al.*, 1984), but European taurine breeds have no resistance, and even Zebu cattle imported from other regions of the continent do not thrive in the humid tropics of West Africa occupied by tsetse flies, vectors of trypanosomiasis (Eisler *et al.*, 2014). Moreover, in the subtropical climate zone, with seasonal rainfall patterns that do not permit continuous vegetation growth, Zebu and Sanga cattle are more resistant to ticks and tick-transmitted diseases as well as feed scarcity and seasonal high temperatures (Berman, 2011).

In Ethiopian, crossbreeds have been benefiting smallholder farmers due to their fast growth. A higher price of Awassi crossbreeds (about double) compared to locals

under farmer management is a clear indication of benefit. Similarly, in Kenya, crossbreeding between Dorper and Red Maasai sheep has been used by a majority of farmers in Kajiado district and are playing an important role for the livelihood of the people (Liljestrand, 2012). However, the presence of genotype by environment interaction on performances of sheep has been well documented in Ethiopia (Getachew *et al.*, 2013; Getachew *et al.*, 2015), Kenya (Zonabend *et al.*, 2014) as well as cattle in tropical countries (Galukande *et al.*, 2013). For example, in Kenya, in the poor environment both local and crossbreds had about the same body weight whereas in the other site (better environment and market-oriented farmers) Dorper and crossbreds had superior weight (Zonabend *et al.*, 2014). Those variable research results on the performance of crossbreeding based on location, genotype and management suggested that the importance of differential recommendations for different locations and careful delineation of crossbreeding area. While promoting highly productive genetics to address climate change will reduce GHG emissions in some ways, maintaining biodiversity and the genetic resources of locally adapted breeds will be needed to complement other climate change mitigation strategies and to ensure the animals thrive (Thornton, 2010). A possible solution may be more research and genetic characterization and selection of indigenous livestock breeds, but only with due consideration to welfare.

Conclusion

Climate change imposes potential negative effects on livestock growth, reproduction, survivability and quality and quantity of related products such as meat, milk, and wool. Identification and conservation of livestock breeds more tolerant of heat stress conditions would be an important progression towards breeding better-adapted breeds to future challenging climates. Phenotypic traits such as coat color type, pattern, hair characteristics, and tail type are possible sources of variation for heat tolerance. Identification of specific gene loci conferring thermotolerance in indigenous livestock breeds could be important for crossbreeding and selection for the favorable allele using phenotypic traits or molecular markers. Scientific research results demonstrated that heat tolerance is a heritable trait and there is variation within/between livestock breeds, and this heritability and variability opens the window for selection of thermo-tolerant animals. Therefore, the combined genomic selection using genome-wide DNA markers that predict tolerance to heat stress and phenotypic selection could be accelerated breeding of highly productive and heat tolerant livestock breeds. Currently, the feasibility of genome-based selection investigated for dairy cow only, but it should be investigated for all livestock breeds. Further research should be conducted on characterization, identification, and conservation of indigenous breeds at a molecular level and on the identification of responsible genes/genomic regions associated with thermoregulation (heat tolerance), feed and production efficiency in order to develop suitable adaptive and mitigation strategies to counter-attack environmental stresses.

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