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REVIEW

Heat tolerance level in dairy herds: a review on coping strategies to heat stress and ways of measuring heat tolerance

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Abstract Tolerance to heat stress is worth noting considering the constant increase in the ambient temperature and high productivity that elevates the likelihood of heat stress in the dairy herd. Besides exposure to hot temperatures, increase in performance of dairy cows is positively related to heat load which results in heat stress. This necessitates the need to incorporate heat tolerance in the breeding objectives. Measuring heat tolerance is still a challenge and might be complex to assess in the dairy herd. Through regressing phenotypic performance of temperature–humidity index (THI), heat tolerance can be assessed. However, the use of the same THI across region might not be effective due to the differences within and among breeds in either same or different herds. The reason being the differing cow's (*Bos taurus*) adaptive and productive response to increasing THI value across different areas. There is vast information about the THI values from the tropics and the temperate regions, however, there is still a gap for THI values for semi and arid places under the pasture-based system. Understanding the coping strategies by the dairy cow to heat stress is important. Various studies have outlined much on the coping strategies but there is still a need to relate the homeostatic and acclimation responses to tolerance to heat stress. This review focusses on discussing the heat stress coping strategies in relation to heat stress tolerance and the ways of assessment in a dairy herd.

Keywords: animal welfare, coping strategies, cows, phenotypic performance, temperature–humidity index, tolerance to heat stress

Introduction

Tolerance to heat stress is the adaptive process ensured by animals to withstand or counter the effects of risen ambient temperature beyond the temperature humidity index (THI) limit of thermal neutral zone. Previous study noted that increased sensitivity in dairy cows (*Bos taurus*) is associated with increased production as a result of lowered THI comfort threshold under high temperatures, this implies that less sensitive cows to high temperatures are more tolerant to heat stress (Bernabucci et al 2014). However, heat stress sensitivity is more influenced by environment than genetics (Boonkum et al 2011). Various expression of heat tolerance includes the extent of decrease in milk, fat and protein yield as the THI rise beyond the comfort threshold (Nguyen et al 2016). Tolerance to heat stress — known as resistance to heat stress is noted to be a trait of economic importance (Sánchez et al 2009). Further elaboration can be made on the heat tolerance level in two ways. Heat tolerance level is a measure of the extent of decrease in performance by an animal as a result of exceeding the comfort threshold (Nguyen et al 2017). Secondly, the THI value at which decline in performance begins can be also used to define the heat tolerance level in dairy cattle. Dairy cows that are tolerant to heat stress — have higher THI limit at which decrease in performance begins and have a slower rate of decline in performance after the THI limit. Therefore, those that have either rapid decrease in performance after reaching the THI limit or lower THI limit are said to be less tolerant to heat stress.

Most dairy farmers prefer high milk producing breeds (i.e. Holstein–Friesian and Jersey) as more high yields are associated with high profitability. However, high production in dairy cows comes with a price of heat stress. The straining effect from heat stress is more likely since there is a negative genetic relationship between heat tolerance and production traits for instance milk, protein and fat yield (Bohlouli et al 2013; Nguyen et al 2017). Further, heat stress burden on the cows is more likely due to the constant climatic change and global warming (West 2003). High metabolism generates large quantities of endogenous heat for instance production of milk by high producing cows is associated with high metabolic heat (West 2003). Therefore, lactating cows are at risk with respect to heat stress and more heat is to be dissipated in order to maintain body thermal balance. A recent study by

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Yan et al (2016) stated that straining effect in the body heat dissipation results when the air temperature is above the comfort threshold, leading to an increase in the net energy for maintenance. There is genetic differences among dairy cattle for the trait of tolerance to heat stress (Bohlouli et al 2013). Genetic difference can be used as a tool in selection of animals that are more tolerant to heat stress (Bernabucci et al 2010). The animal's tolerance to heat stress capabilities is contributed by the ability of that animal to adapt to an environment. The differences in the morphology is important and it has a greater contribution as far as tolerance to heat stress is concerned (Salama et al 2014). In addition, findings reported by Gantner et al (2017) showed that Holstein–Friesian are less tolerant to heat stress. More so, Holstein–Friesian breed is a heat sensitive breed and under performance is expected when the cows are kept in the tropic regions (Lee et al 2016). According to Salama et al (2014), animals with lower body weight are more tolerant to heat stress — this implies that the jersey breeds and some of the crossbreeds are more tolerant to heat stress as compared to the Holstein–Friesian. Furthermore, small body weight have larger surface ratio hence this allows faster rate in the dissipation of internal heat. Jersey cows are said to be more tolerant to heat stress than other breeds (Bernabucci et al 2010), due to their more efficiency in internal heat dissipation by greater sweating rate (Salama et al 2014).

Previous study by McManus et al (2009) noted a rise in worries related to heat tolerance for dairy in the temperate region. This necessitates the need for inclusion of the heat tolerance traits in the selection of dairy herd. Various studies have mentioned the challenges associated with the selection of heat-tolerant animals (Sánchez et al 2009; Macciotta et al 2017). Besides the challenges in measuring tolerance to heat stress, tolerance remains an easy concept to understand. However, Sánchez et al (2009) highlighted the regressing phenotypic performance of THI as an indirect alternative for measuring heat tolerance. More so, variation in production traits performance under hot areas can be used in assessing heat tolerance (Smith et al 2013; Hammami et al 2015; Nguyen et al 2016). It is worth noting that heat-tolerant cows might not be cold resistant and vice versa hence, estimation of heat stress from weather data obtained (i.e. for cold tolerant cows) in a temperate region, on other regions might raise questions (Carabaño et al 2016a). The assessment of heat tolerance level among dairy cows is a tool for breeders in the selection of cows with superiority with respect to heat tolerance. Variation prevails among dairy cows across regions with regards to tolerance to heat stress hence, this review relates the heat stress coping strategies to heat tolerance and the ways of assessment in a dairy herd with emphasis on Holstein–Friesian and Jersey breeds.

Methods

The literature review of heat tolerance level in dairy herds considering coping strategies to heat stress and ways of measuring heat tolerance was done successfully with the aid of the University of Fort Hare (UFH) library databases. Four databases were searched from the UFH that included Academic Search Complete (EBSCOhost), Agricola (EBSCOhost), ProQuest Agriculture Journals and Science Direct. Adding to the list Google scholar was utilized as well and having the majority of the journals from ProQuest Agriculture Journals and Science Direct. Search terms were ('heat tolerance', 'heat stress') AND ('heat stress coping strategies' OR 'acclimation'). Genomic selection articles were also included in this review. In addition, the literature search yielded 82 articles as listed in the reference list.

How tolerance can be of importance to heat stress

With regards to economic losses St-Pierre et al (2003) highlighted that heat stress affected the dairy herd more as compared to other livestock industries. Report by de Andrade Ferrazza et al (2017) encouraged producers to have ability in predicting the effects of the environmental conditions on the dairy herd. This is important due to the fact that animal welfare is ensured and this also encourages performance and increase in profitability. Globally, heat stress is one of the increasing problem facing the dairy industries (Polsky and von Keyserlingk 2017). Due to climate change there will be intensified exposure of the dairy cows to heat stress (Gauly et al 2013). This is of more concern for those dairy cows that are kept outdoor under pasture–based systems. Dairy herd kept under pasture–based systems have more period of time been directly exposed to ambient climatic conditions and direct exposure to high ambient temperature leads to excessive internal heat load (Ammer et al 2016). In addition, poor performance and death may result due to the effects of heat stress. Previous study by Segnalini et al (2013) emphasized the adoption of appropriate adaptation strategies as a way of countering the effects of heat stress among dairy cows. Findings reported by Nguyen et al (2016) revealed increase in cost of management and loss of income due to the response towards heat stress.

Heat stress can take place in dairy cows even though the cows are subjected to normal ambient temperatures that favour a thermal neutral zone (Gantner et al 2017). This is caused by the increase in production which result in the production of more basal metabolic heat (Bernabucci et al 2010; Santana et al 2015). Increase in heat sensitivity by the dairy cows is directly proportional to the increase in milk yield (Gantner et al 2017). Holstein–Friesian is the common dairy breed used in many dairies due to its high milk producing ability — hence it is worth noting that the breed is heat sensitive and decrease in performance results if exposure to hot ambient temperatures is prolonged. To prevent losses in production, management practices such as physical modification with the use of shades and sprinklers and selection of heat tolerant breeds can be implemented (West 2003; Fournel et al 2017). The use of shade might not be practical due to concentrated rotational grazing on some pastures. In addition, the use of sprinklers (Bernabucci et al 2014) is not practical as well due to lack of water in some areas (Nguyen et al 2016). On the other hand, crossbreeding the dairy breeds with the local adaptive breed (ie high adaptability traits including heat tolerance and tick bite) is not compelling due to drastic decrease in the yield capability (Sánchez et al 2009). More so, a negative genetic relationship exist between milk yield and tolerance to heat stress (Macciotta et al 2017). Variability exist among and within Holstein–Friesian and Jersey herds with regards to heat tolerance. In addition, estimates of tolerance to heat stress can be constructed from the weather records and measured milk yield (Nguyen et al 2016). Heat tolerance level can be obtained by measuring the extent of decrease in milk yield as the THI rise beyond the comfort threshold (Nguyen et al 2017). In a nutshell, assessing the heat tolerance level helps in identifying superiority with regards to heat tolerance between and within Holstein–Friesian and Jersey herds.

The consideration of tolerance to heat stress traits is of importance under the dairy industry due to its influence on the consistency in the food supply for consumers. In other words, producers must consider tolerance to heat in the herd so that demand by consumers can be reached. Heat stress influences farm productivity in a negative way hence jeopardizing the consumer food supply chain (Bernabucci et al 2010). Deterioration of the tolerance to heat stress can be prevented effectively by timely choosing heat-tolerant cows and a positive correlation exists between heat tolerance and fertility (Nguyen et al 2017).

Assessing heat tolerance level in a dairy herd

Direct measures of a cow's ability to reproduce, produce and survive under heat stressing conditions are noted to be a potentially helpful way for selecting animals for tolerance to heat stress in hot regions (Boonkum et al 2011; Hammami et al 2015). Some of the physiological parameter used includes heart rate, respiration rate (Bernabucci et al 2010; Cardoso et al 2015), body temperature and rectal or vaginal temperatures (Ammer et al 2016). However collection of this physiological parameter requires restraint and handling procedures. Restraining the dairy cows might cause some stress response and this increases experimental error. In contrast, rectal and vaginal temperatures that are obtained by manual recording, are still the best methods in determining the body temperature of the cows (Ammer et al 2016). Heart rate can be obtained by stethoscope, the digital–meter can be used to record rectal temperatures and the respiration rate can be obtained through visual observation of the flank movement per minute (Cardoso et al 2015).

The manual recording means in collecting the physiological parameter is labor intensive especially at a commercial setup and this might result in more operator error and animal injuries (Ammer et al 2016). Suggestions from Cardoso et al (2015) noted the use of thermographic images in measuring the cow's body temperature. On the other hand, the use of intraruminal sensors is noted to be a better alternative to measuring cow's body temperature (Ammer et al 2016). In addition, the sensor is placed in the reticulum to measure temperature on a continuous basis. However, water intake and fermentation can influence the temperature measurements (Liang et al 2013).

Measures of heat tolerance in dairy herds

Temperature–Humidity index as a measure of heat tolerance level in a dairy herd

Temperature–humidity index is a value that combines the effect of temperature and humidity on the risk of heat stress and has been widely used for years in studies related to heat stress. According to Bohmanova et al (2007), THI is applied as a safety index in reducing and monitoring the loses that results from heat stress. Furthermore, other researchers suggest that THI is a heat stress indicator that is used worldwide (Bohlouli et al 2013), and common bioclimatic index (Bernabucci et al 2014). Recently, THI is applied in the evaluation of the Livestock Weather Security Index (LWSI) and this helps to identify whether the environmental conditions are favorable for animal comfort and welfare (Domínguez-Mancera et al 2017).

Various findings showed that the detection of heat-stressed dairy cows is successfully done through the use of THI (Salama et al 2014; Xu et al 2018). In addition, the differences within the same breed and between dairy breeds could be accounted for by the THI in a better way (Bohlouli et al 2013). This implies that THI is more applicable to the modified pasture-based farming system that deals with dairy herd exposed to a similar environmental condition under the same management techniques. Furthermore, the use of THI is the most standard and practical method for application in the animals especially dairy herd (Testa et al 2017). However, there is a lag in research on heat tolerance levels as far as THI is concerned.

The temperature and humidity records can be accessed easily from meteorological weather stations. Measurements from the wet and dry bulb thermometers are used in the calculation of the THI index which is utilized as an estimate of heat stress (Dikmen and Hansen 2009). In addition, the wet-bulb thermometer is used as an alternative way of determining humidity indirectly (Xu et al 2018). Regressing the THI on the performance data such as milk yield aids in the determination of the tolerance to heat stress (Wildridge et al 2018). Many studies reviewed a negative correlation between the THI and the performance data (Carabaño et al 2014; Santana et al 2015; Nguyen et al 2016, b; Wildridge et al 2018). On the same note, previous studies suggest that heat stress in dairy cows starts when THI exceeds 72 (Dikmen and Hansen 2009; Könyves et al 2017). There is a variation on the critical temperatures for each individual cow (Könyves et al 2017) and extent of acclimation been one of the factors causing differences. Temperature from the dry bulb is the limiting factor for tolerance to heat stress in dry climate regions (Bernabucci et al 2014). In humid places, the relative humidity was the limiting factor as well. Combination of the THI and day test record can be a useful tool in the estimation of the genetic component of tolerance to heat stress. Productive dairy cows that are less sensitive to the increase in the THI (ie high temperatures) could be identified through modeling performance as a function of a continuous THI (Hammami et al 2015).

Broken line model as a measure of tolerance to heat stress

Broken line model describes the cow's productive response to rising heat load (Carabaño et al 2016a). The heat load also known as the heat content is the heat the animal carries at a given time. This heat results from metabolism and also gained from the environment excluding the dissipated heat. Dairy cattle are assumed to have a thermal comfort zone within no response to rising ambient temperature is expected (Carabaño et al 2016a). This model categorizes the THI into groups that is a thermal comfort zone and the discomfort zone.

Various studies claimed that the upper threshold for the thermal comfort zone is 72 (ie THI value) and after which a decrease in performance is expected due to the effect of heat stress (West 2003; Santana et al 2015; Carabaño et al 2016a; Macciotta et al 2017; Kaufman et al 2018). This implies that increment in the THI within the comfort zone has no effect on the dairy herd performance. However, the decline in performance might be a result of other thermal comfort zone factors that includes body traits and coat (Könyves et al 2017). The upper limit of the discomfort zone is 76 above which the cow enter an alert condition of intensified heat stress. In addition, a further increase in the THI results in the death of the animal. The model is too simplistic and the response by the dairy cows differed across places (Carabaño et al 2016a).

Assessing heat tolerance level using the random regression model

Random regression model (RRM) involves regressing phenotypic performance of THI without defining the thresholds. It is the common way of analyzing the longitudinal data (Aguilar et al 2009). More so, longitudinal data are data involving repeated observations for an outcome variable (Zeger and Liang 1986), for an instance milk yield in the dairy herd. There is greater flexibility of using the RRM and it has a better reflection on the covariance structure of the permanent effects hence results in higher accuracy (Brügemann et al 2011). Measuring tolerance to heat stress seem difficult, however, genetic evaluation is effectively possible through the use of RRM (Sánchez et al 2009). Previous studies mostly applied the RRM in genetic analysis (Bohmanova et al 2008; Aguilar et al 2009; Brügemann et al 2011).

The genetic component of tolerance to heat stress can be estimated by combining the THI and the performance data (ie test day records for milk yield traits) (Nguyen et al 2016). Previously, Brügemann et al (2011) noted modeling of additive genetic random regression effect on tolerance to heat stress by incorporating the decrease of milk yield as a result of heat stress beyond the selected threshold value. In addition, the phenotype for tolerance to heat stress can be denoted as a decline in milk production (Nguyen et al 2016). This implies that heat tolerance can be assessed through regressing the performance data (ie records of the extent of decrease in milk yield under heat stress) as a function of the THI (ie above the comfort threshold) (Hammami et al 2015). According to Bohlouli et al (2013) worth noting genetic variability for tolerance to heat stress of production traits can be obtained by using regressing on a function of THI. Various studies noted flexibility in statistical modeling by applying the RRM and there will be no need for defining specific thresholds (Brügemann et al 2011; Bohlouli et al 2013). Ravagnolo and Misztal (2000) estimated the additive variances resulted from heat tolerance and production effects and explored the chances of increased heat tolerance selection in the future. They noted that the dynamics of heat stress throughout lactation can be captured by the use of RRM. However, this will be at a cost of greater model complexity. Findings reported by Bohlouli et al (2013) revealed that changes in genetic variance and covariance components can be studied over the whole trajectory of a covariate (ie time-dependent) such as days in milk. In addition, a THI dependent covariate is applicable as well (Brügemann et al 2011). Random regression models can create either variance or covariance components for all combinations present (ie THI and days in milk) without defining the thresholds and heterogeneous additive genetic variances can be accommodated during lactation (Bohlouli et al 2013). In comparison with the repeatability model, RRM can bring forth higher accuracy (Ravagnolo and Misztal 2000). Regressing the performance after the threshold is a useful tool in modeling for additive genetic variance, however, other findings suggest that RRM contains some inaccuracies at different test day data and at the end of lactation, it shows unreasonable high variances which could result in bias evaluation (Bohmanova et al 2008).

Hierarchical Bayes model as a measure of heat tolerance level

The level of tolerance to heat stress varies among dairy cows, due to the difference in response to the increase in ambient temperature beyond the thermal comfort threshold. The hierarchical Bayes model (HBM) is a more realistic way of measuring tolerance to heat stress among dairy cows with differing responses to rise in ambient temperature (Sánchez et al 2009). Modeling the additive genetic variance for tolerance to heat stress by phenotypic regression of the performances after the comfort threshold — seems to be effective (Hammami et al 2015). This approach usually assumes that all the cows have the same threshold and the extent of decline in different places and over time. The idea of a constant THI threshold might not be realistic. Fortunately, HBM conquers the above limitation with an assumption that both the threshold and the rate of decline varies among individual cows within and across regions (Hammami et al 2015).

Hierarchical Bayes Model (HBM) defines the animal's level of tolerance to heat stress as the extent of decrease in performance by a cow beyond an unknown THI threshold and THI value at which decrease in performance begins due to heat stress (Sánchez et al 2009). In support, Sánchez et al (2009b) noted that the model postulated that there is no environmental effect until an unknown THI value is exceeded for every individual cow with data. In addition, they noted that the HBM favors the partitioning of variability (ie on the threshold) for each cow into genetic and environmental components. The higher the THI value at which decline in performance begins the slower the decrease rate when heat stress commences and the more heat tolerant the cow is to heat stress (Sánchez et al 2009). Findings reported by Nguyen et al (2016) concluded that dairy cows with a higher threshold would also have a lower decline rate in performance. The differences in individual deviations from the average response can be determined by the variability in heat stress thresholds and the extent of the negative heat stress effect within the dairy herd (Carabaño et al 2016a). Applying the same knowledge, cows noted to have the lower rate of decrease can be automatically considered to have higher THI thresholds of response to high ambient temperatures. Genetic selection of tolerance to heat stress cows relies on the determination of these individual deviations.

A recent study noted the suitability of HBM for meta-analysis and such study gives room for inclusion of own set of parameters (Moraes et al 2017). Apart from that, greater flexibility can be provided by HBM as compared to the traditional reaction norm model because semi-parametric form of reaction norm function is allowed (Sánchez et al 2009b). This holds with Moraes et al (2017) who further outlined that the parameters follow a distribution whereby the vector means is a set of parameter common to every study. However, the HBM assumption might require very complicated and highly parameterized models and this can make estimation procedures inefficiency (Hammami et al 2015). More so, Sánchez et al (2009) noted high computing cost for different threshold estimation per herd, seasons and year.

Coping strategies to heat stress by dairy cows

Heat stress has a greater influence on the thermoregulatory mechanisms (de Andrade Ferrazza et al 2017). It is a straining condition which begins when the body temperature is elevated beyond the animal's coping strategies. The causes of heat stress include a combined effect of temperature, relative humidity, radiation, precipitation and air movements (Bohlouli et al 2013). Production and accumulation of heat together with ineffective cooling results in heat load in the cow and this generally cause body temperature increase (West 2003). More so, heat stress is an effect of climate or productive response by the dairy cow (West 2003). Variability in response by cows exposed to heat stress suggested an adaptive response (de Andrade Ferrazza et al 2017). Furthermore, there is variability in the activation of the thermoregulatory mechanism which relays on the time spent under harsh temperatures and this has an accumulative effect on the response. A recent study by Gao et al (2017) noted changes in behavior and metabolism in heat stressed cows.

Homeostatic response by dairy cow under heat stress

Homeostatic response happens soon after the detection of the rise in the internal body temperature. According to Kadzere et al (2002), the response can take place within seconds or minutes and dairy cows engage homeostatic processes with the goal of maintaining normal body temperature. Homeostasis is the process of maintaining internal condition of the animal's body within a range that the body can sustain life (Starr et al 2009). In addition, the key aspects of homeostasis includes detection and response to the altered internal conditions for instance change in internal body temperature beyond THI comfort threshold. Dairy cows like any other homeotherms are adapted to function under optimum range within respective thermal neutral environments and alteration in the surrounding conditions threatens the normal balance in metabolism (Kadzere et al 2002). The initial homeostatic response to heat stress involves increased sweating, water intake, respiration rates, reduced feed intake and heart rate (Bernabucci et al 2010). However, increase in respiratory and heart rates was noted to be temporary and the rate are reduced in the situation that heat stress persist (Kadzere et al 2002). A study by Polsky and von Keyserlingk (2017) described the responses as physiological coping strategies. These responses assist in decreasing the heat stress by increasing heat dissipation. Homeostatic response to heat stress in cows (mammals) also involves reduced urinary and faecal water losses (Kadzere et al 2002). In high temperature regions, efficiency of heat dissipation is of utmost importance in the maintaining of a normal animals' body temperature. The evaporative cooling in dairy cows is inevitable especially when the cows are under increasing high ambient temperatures (Hansen 2004). In addition, the relevance of sweating and pulmonary heat loss (ie that relays on the respiratory rate) which assist in heat dissipation in warm-blooded animals (Pereira et al 2014). The animal's ability to dissipate metabolic heat is decreased by rise in the ambient temperature and humidity. However, higher respiratory rate in cows under high temperatures relates to low tolerance to heat stress (Pereira et al 2014). This holds with findings reported by Cardoso et al (2015) that physiological parameters such as respiratory rate and body temperature, can be useful in determining tolerance to heat stress and adaptability evaluation in animals.

Acclimation response in relation to tolerance to heat stress

Prolonged thermal load on the dairy cows results in acclimation to heat stress. The effects of the increase in ambient temperature do not happen instantly instead the effects take place after a delayed time period (West 2003). Acclimation to heat stress is the ability of an animal to adjust its physiological mechanism in order to cope with extreme environments (Schwimmer et al 2004), which needs days or weeks to occur (Bernabucci et al 2010). Figure 1 gives a summary of the acclimation responses. Previous study Horowitz (2002) noted induced adaptive alterations that boost the ability to endure harsh temperatures. In addition, acclimatory homeostasis is the mechanism which positively brings about heat acclimation. This process imposes adjustments on the physiology, behavior and metabolic reactions in order to reduce the heat strain effect on the animal (Bernabucci et al 2010). This physiological and metabolic modification takes place in the central and peripheral tissue of the animal's body with the goal of enhancing the ability of thermoregulatory effectors to endure heat stress. All in all, the major effect of acclimation responses by an animal, to achieve a new equilibrium that can be taken as the new physiological state through metabolism coordination (Bernabucci et al 2010).

Physiological adaptive mechanism to heat stress

The adjustments in the physiological coping strategies include changes in the endocrine system. Evolution in these physiological mechanisms is noted in cattle, for instance, some cattle developed an increased core body temperature, respiratory and endocrine changes (de Andrade Ferrazza et al 2017). According to Lee et al (2016), the disorders in the endocrine system in Holstein cows were caused by the effects of high temperatures. In addition, a disorder of the endocrine system leads to high temperature and changes in secretion rates of hormones.

Changes in the endocrine system for instance in the thyroid status also affect the metabolism. The presence of thyroid hormones in the blood is an important determinant of metabolic rates (Kahl et al 2015). This is worth noting in the adaptation to heat stress. Other altered endocrine hormones due to heat stress include growth hormone and it is reduced together with glucocorticoid levels and catecholamine (Bernabucci et al 2010). More so, thyroid hormones are important for the regulation of thermogenesis. The thyroid hormones play important role in controlling metabolic processes, growth, and development. In addition, the release of the thyroid hormones is controlled by the hypothalamus via a negative feedback mechanism. The hypothalamus which is located in the brain works as a major integrative control center for maintaining normal constant body temperature (Salama et al 2014). Triiodothyronine is the most active hormone in metabolic processes (Kahl et al 2015). The function of thyroid hormone is to give rise in metabolic activity of tissues around the body and this results in the production of more metabolic heat. In support, Ocak et al (2009) mentioned that oxygen utilization and production of heat by cells is stimulated by the thyroid hormones and results in increased basal metabolic rate. In addition, the hormones also interfere with the number of nutrients partitioned for maintenance (Kahl et al 2015).

Higher levels of thyroid hormone in the blood are associated with heat intolerance (Starr et al 2009). When cows are subjected to heat stress conditions, the concentration of thyroid hormone is decreased in order to reduce heat production. Hence there is reduced circulation of the thyroid hormones concentration under heat stressing environments (Kahl et al 2015). Cattle breeds that have a higher tolerance level to heat stress, have the ability to reduce heat production and lose heat at a faster rate.

Metabolic adaptive mechanism to heat stress

Metabolic disorders result as an effect of heat stress on the dairy cows which includes reduced growth, reproductive rate and decreased milk production (Nardone et al 2010). This might be caused by reduction in feed intake as a result of excessive heat stress. More so, protein and energy metabolism is also negatively affected by excessive heat (Koch et al 2016; Yan et al 2016). Reduced growth rate and milk production results in low metabolic rates (Cardoso et al 2015). Energy metabolism in cows is influenced by the dietary energy together with heat stress. Apart from the strain caused by heat stress, more dietary energy is partitioned for the maintenance of the body and less energy is channeled towards production (Yan et al 2016). In other words, the net energy for maintenance is maximized under heat stress conditions. A study by Hammami et al (2015) mentioned feeding modifications in the dairy herd as a method of countering the effects of heat stress. Feeding energy diet rich in lipogenic nutrients favors production of milk and this results in more basal metabolic heat produced. On the other hand, feeding of energy diets that contain more glycogenic nutrients results in more nutrients channeled towards body reserves (Yan et al 2016). High milk yielding dairy cows have bigger frames and bigger gastrointestinal tracts (Gantner et al 2011). Larger gastrointestinal tracts allow digestion of larger quantity of feed and this is a source of more metabolic heat. Argument by West (2003) noted that the production of metabolic heat in dairy cows raised as a result of an increase in the level of milk synthesis. This implies that high milk-producing dairy cows are more at risk to the effects of heat stress when exposed to high ambient temperature.

Apart from the decreased energy expenditure, metabolic adaptation to heat stress also includes an alteration in the post-absorptive metabolism. There is a shift in the nutrient partitioning which favors a reduction in the production of endogenous heat (Koch et al 2016). High ambient temperature necessitates a metabolic response. However, metabolic responsiveness relays on the physiological state of the animal (ie the stage of lactation for instance). In addition, the difference in metabolic adaptation to heat stress between lactating cows and late pregnant cows was noted (Bernabucci et al 2010). In early lactating cows under heat stress, the metabolic adaptation mechanisms governing the reduction in the production of endogenous heat involves an alteration in the substrate utilization for energy (Koch et al 2016). Further, gluconeogenesis and glycogenolysis are increased to supply glucose which is then used for milk production (Loor et al 2005). There is a reduction of heat production from fatty acids and a shift towards glucose metabolism in the production of energy in lactating cows experiencing heat stress (Koch et al 2016). In support, West (2003) stated that there is a lack of adipose tissue mobilization in animals that were experiencing heat stress. The shift in substrate utilization takes place in the liver and skeletal muscle and this is essential to maintain gluconeogenesis of milk production in early lactation (Koch et al 2016). In dairy cows that are experiencing heat stress, lactate and alanine utilization increases for the synthesis of glucose (Shahzad et al 2015).

Apart from changes in energy metabolismo, heat stress has an effect on protein metabolism as well. When the cow is heat stressed the breakdown of muscle protein takes place, therefore reducing the capacity of the muscles to oxidize fatty acids (Koch et al 2016). This forces the muscles to depend on the glucose in the circulating blood and the glycogen reserves for energy (Koch et al 2016).

Behavioral adaptive mechanisms to heat stress

Exposure to high temperatures cause some changes in both the physiological and the behavior of the dairy cows. Prolonged exposure to higher ambient temperature necessitates acclimation. Acclimation to heat stress results in some changes in the behavior of the animal and these are behavioral coping strategies (Polsky and von Keyserlingk 2017). Some behavioral changes in animals under hot environmental conditions involved searching for shade and increased time of standing. Dairy cattle are ever ready to utilize shade upon given an opportunity (Schütz et al 2010). In addition, the need for shade increases with increase in ambient temperature. Dairy cattle tend to spend much time under shade and can be very aggressive when the shade is limited. This reduces feed intake since the cow is standing and the reduction in feed intake assist in reducing the production of metabolic heat. Heat increment as a result of feeding in ruminants is an important source of heat production (Kadzere et al 2002).

Unshaded cows show greater response and more behavioral coping strategies than those having shade. Findings reported by Schütz et al (2010) noted increased time spend around water troughs and more standing in unshaded dairy cows. In addition, cows under high temperatures tend to have some alteration in the grazing habit as well and this includes shifting of the grazing time to cooler periods of the day (Gauly et al 2013). Dairy cows that are more tolerant to heat stress continue grazing for longer periods of time even though heat stressed and having a high respiratory rate (Pereira et al 2014).

Coping strategies to heat stress within cells

Various studies noted the coping strategies to heat stress at the cellular level (Parcellier et al 2003; Arrigo 2007; Nigam et al 2018). Heat stress and shock in cells are caused by exposure to high temperatures ending up decreasing lymphocyte viability, inducing a larger alteration in the gene transcription and changes in protein synthesis (Lee et al 2016). In response to heat stress, cellular homeostasis involves the induction of heat shock proteins (HSP). Heat shock protein is a stress protein that is highly conserved. In addition, other stresses besides heat stress are capable of inducing the heat shock protein (Parcellier et al 2003). A recent study by Nigam et al (2018) classified the heat shock proteins into groups basing on their variation in molecular weight that is HSP 100,90,70 and 60. In addition, these proteins are simply grouped as high molecular weight and small HSP. Das et al (2016) reported the changes that occur during gene expression of HSP under thermal stress. These changes comprise of heat shock transcription factor 1 activation; increase in HSP gene expression and a decrease in other protein expression and synthesis; rise in glucose and amino acid oxidation; reduced metabolism of fatty acid; activation of the endocrine system to induce stress response and activation of the immune system via extracellular secretion of HSP. They further noted that acclimation (ie altered physiological state) could result if heat stress persists.

Heat shock protein beta-1 play a major role in cytoprotection and resistance to heat stress during stress conditions (Nigam et al 2018). The HSP beta-1 plays a great role in the cell survival and it assists in development and differentiation of cells. In addition, HSP beta-1 is capable of modulating reactive oxygen and increases glutathione levels hence resulting in the protection of the cytoplasm. Previous study by Parcellier et al (2003) observed refolding of non–native proteins due to the interactive effect of the HSPs. Furthermore, under chemical stress, the HSP acts as an anti-apoptosis agent which interact with the mitochondrial-dependent and independent pathways of apoptosis. All in all, the HSP enables cells to gradually adapt to heat stress (Arrigo 2007). Further, during hot periods the responsiveness of the HSP is increased resulting in a greater expression. There is genetic variation in cellular resistance to increased temperature in dairy cows. Thermotolerance genes are present in the cattle breeds (Hansen 2004). Genes conferring cellular thermotolerance (ie HSPs) could be identified and they can be of great use. There is the possibility of transferring thermotolerance genes to heat-sensitive breeds with the goal of improving some physiological systems compromised by heat stress (Hansen 2004). However, there is still inadequate information regarding the molecular basis for improved tolerance to heat stress at a cellular level.

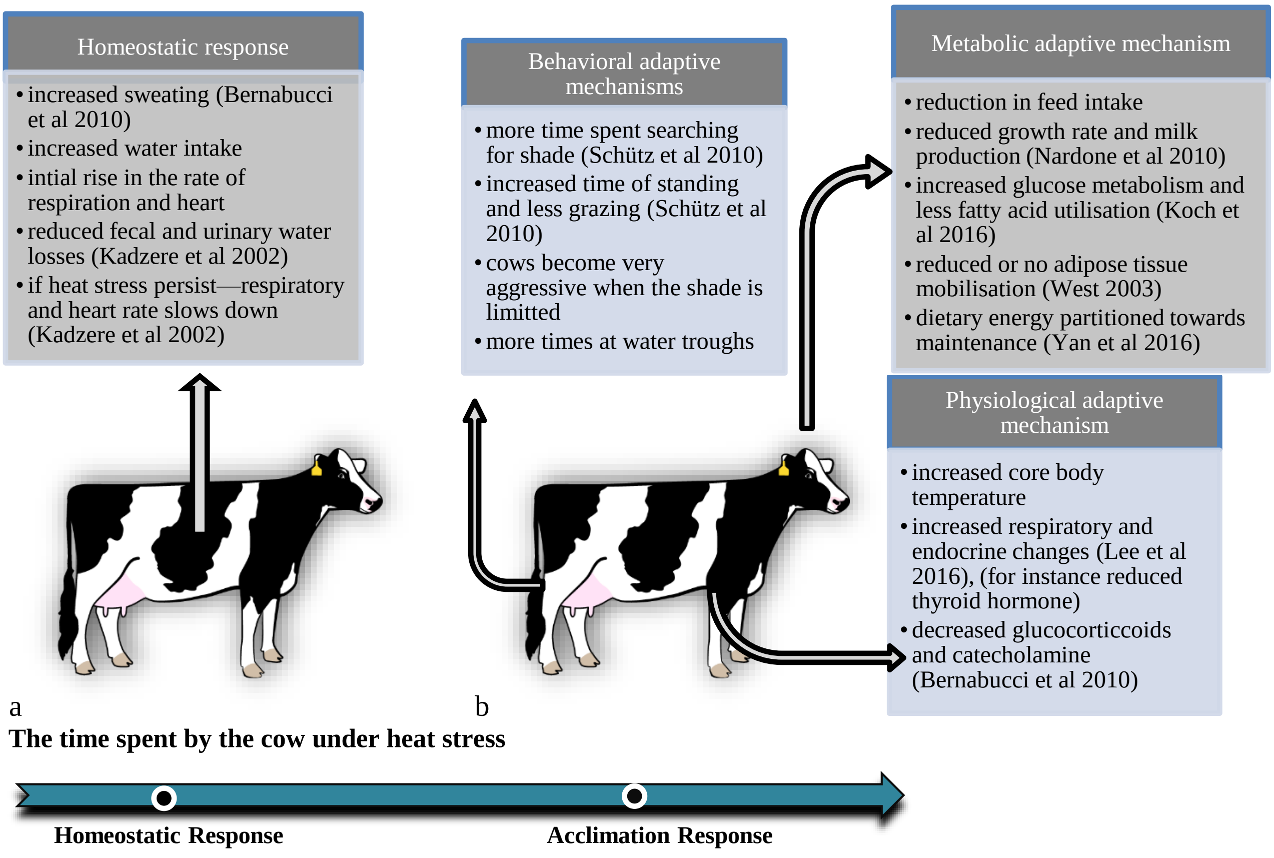

Figure 1 Coping strategies to heat stress by dairy cows. (a) Changes due homeostatic response which commences soon after detection of change in internal body temperature; (b) Alteration resulting from acclimation response to heat stress. Prolonged exposure to higher ambient temperature neccesitates acclimation.

Is genetic and genomic selection of use in improving tolerance to heat stress in a dairy herd?

Many studies have noted production losses and mortality as a result of heat stress (St-Pierre et al 2003; Hammami et al 2015; Koch et al 2016). Different farmers came up with varies countermeasures which include feeding modifications, environmental modification, and selection of heat tolerant cows (Renaudeau et al 2012). These strategies are still the best ways in the alleviation of heat stress (Hammami et al 2015). Some environmental conditioning such as shades, fans, and sprinklers are too expensive and not applicable to pasture-based dairy farms and changes in feeds best suits confined herd. In addition, these environmental modifications are not justifiable economically and are associated with difficulties with regards to sustainability. From the three strategies, genetic selection of heat tolerance dairy cows remains the only feasible method for many farmers.

Genetic selection of heat tolerant dairy cows

High productive dairy breeds are commonly used in various dairy industries. However, to a greater extent, the adaptability with regards to heat tolerance of the dairy herd to some environments remained a limiting factor. The performance of dairy cows is affected by their response to stress experienced in the environment and more production is achieved by the best-adapted cows in that particular environment (i.e. environmental flexibility) (Misztal 2017). More so, adaptability alludes to how best a cow copies up with the environmental stresses specifically heat stress. Variability exists in the onset of heat stress with respect to daily milk production among the Holstein–Friesian (Sánchez et al 2009). In addition, portions of the variability contain a genetic origin that can be used in genetic selection programs for tolerance to heat stress (Sánchez et al 2009). Selection of heat tolerant dairy cows is an effective way in the management of heat stress under the condition that high production efficiency can be associated with the ability to resist hot temperatures experienced in the environment (Hammami et al 2015). However, the effectiveness of the selection strategies requires accompaniment with commercial data and continuously improved management (Misztal, 2017). The previous study noted that a combined selection is possible for tolerance to heat stress and production (West 2003). On the same note, genetic selection for heat tolerant cows is a suitable way of reducing infertility and low dry matter intake problems (Santana et al 2017). Genetic selection can assist in identifying superior heat tolerant animals, though few cycles are required to achieve clear results (Misztal 2017). Genetic improvement of the dairy herd and livestock, in general, is cost effective because it brings forth to permanent and cumulative change (Wall et al 2010). In support, Katiyatiya and Muchenje (2017) stated the merit of breeding animals that can adapt so as to maximize the production capacity. However, crossbreeding the high productive breeds with breeds that are heat tolerant is unappealing due to the drastic reduction in performance. Alternatively, crossing the dairy breeds (i.e. Jersey and Holstein–Friesian) has a greater potential in the dairy industry (West 2003).

There is a negative relationship between the productive traits and THI (Bernabucci et al 2014b). This implies that the more heat tolerant the dairy cow is for instance, the lower the performance with respect to production traits. In addition, crossbreeding with heat-resistant breeds is less common for dairy cattle (Misztal 2017). In addition, selection for production traits solely neglecting heat tolerance results in a decrease in the overall performance by the cows (West 2003; Bernabucci et al 2014a). More so, recent study by Misztal (2017) noted that fitness and robustness (environmental flexibility) can be compromised by only selecting production traits. With the use of pedigree and phenotypic performance records, cows that are heat tolerance can be selected to breed during the breeding periods. Furthermore, due to the differences with regards to thermoregulation, a potential sire that is capable of transmitting important traits can be selected (West 2003). However, the rate of genetic improvement is slow due to the fact that the heritability of the trait (tolerance to heat stress) is low (Nguyen et al 2016). In addition, the long generation interval associated with the trait also contributes to the slow gain (Nguyen et al 2016). All in all, genetic selection is a continuous process and is expected to decrease the environmental footprint of the cows' production per unit of product (Misztal 2017). Hence, deterioration in high tolerance to heat stress can be prevented by monitoring trends of the genetic component of heat stress (Santana et al 2015).

Genomic selection for heat tolerance traits in a dairy herd

Heat tolerance is a trait of economic importance which helps to alleviate the drastic decrease in milk production that would negatively affect productivity and profitability. Constant change in climate and global warming — renders the inclusion of tolerance to heat stress in the selection, paramount important (West 2003; Carabaño et al 2016b). Speeding up the rate of genetic gain for heat tolerance is of great importance in places experiencing high temperatures and due to the effects of climate change (Nguyen et al 2016). The pasture-based system is widely adopted in many dairies whereby rotational grazing is the key feature of the grazing system. Due to the high temperature in some region and especially in summer sheds are ideal in assisting in internal thermal regulation of the animals. On the other hand, construction of sheds around the camps or paddocks to accommodate the herd might be too expensive and space consuming, however, report by Palacio et al (2015) noted the use of portable shades as an alternative. More so, during hot days the animals tend to sacrifice grazing time for the shed. This definitely results in a reduction in production. Therefore this necessitates the need for improvement of heat tolerance traits.

Early biotechnologies (e.g., artificial insemination and multiple ovulation embryo transfers) improved production efficiency (DeJarnette et al 2004). However, less concern was put on adaptability traits (e.g., tolerance to heat stress) and health in favors of improving the production traits (Williams 2005). Further ascertainment of genetic merit was edified through the use of Marker Assisted Selection (Pedersen et al 2009). Marker Assisted Selection influenced genetic progress by increasing the accuracy of selection through the use of more information relating to the genetic makeup of the individual animals. However, Marker Assisted Selection is limited to the use of a single genetic marker which is responsible for a fraction of genetic variation (Wallén et al 2017). All in all, genetic progress is slow as compared to genomic selection.

Genomic selection is a recent promising technique best suited in accelerating the genetic gain of a dairy herd with regards to tolerance (Nguyen et al 2016). Previous study Silva et al (2014) defined a genomic selection in a simple way as the use of genomic breeding values in making selection decisions. Genomic selection involves the prediction of the breeding value of selection animals with the use of genome-wide genetic markers (Meuwissen et al 2001). Furthermore, genomic selection involves the use of Single Nucleotide Polymorphism (SNP) a genetic marker that is distributed throughout the entire genome (Silva et al 2014). All quantitative trait loci (QTL) that have a contribution to the variability of a trait may be captured with the use of the SNP (Silva et al 2014). Genomic selection relies on a linkage disequilibrium between the polymorphisms and the markers that causes differences in the traits of economic importance (Hayes et al 2013). According to Weller et al (2017), the linkage disequilibrium is between the markers and the causative genes. Since the whole genome is captured by the genetic marker, traits of low heritability and adaptability traits are also catered for (Wallén et al 2017). A study by Nguyen et al (2017) noted that tolerance to heat stress can be improved using genomic selection. The extent of decrease in milk production with rising heat stress can be used as an indicator trait for tolerance to heat stress (Nguyen et al 2016). In addition, genomic estimated breeding values (GEBV) for tolerance to heat stress can be obtained with the use of high-density SNP data (Nguyen et al 2017). However, the major problem with respect to GEBV is the assembly of a reference population of the genotyped herd and besides, GEBV for tolerance to heat stress is a necessity if the trait is to be included in selection decisions (Nguyen et al 2016). Fortunately, the extent of decrease in milk production can be used as a phenotype for tolerance to heat stress and this can be successfully obtained at large scale by combing the weather and performance data (Nguyen et al 2016). This can be used to derive a genomic prediction for tolerance to heat stress (Nguyen et al 2016). After predicting the breeding value from the SNP genotype, the cows (ie considered for selection) must be ranked on the basis of the GEBV and the best can be selected (Hayes et al 2013). In support, cow's superiority (ie with regards to heat tolerance) is based on its genetic merit ranking (Silva et al 2014). Hence predictions of genetic estimated breeding values can be done to potential animals at an earlier stage (Hayes et al 2013).

Genomic selection accelerates genetic progress in the dairy herd (Weller et al 2017), the genetic interval can be reduced to two years and predictions of traits that are either expensive or hard to measure (Hayes et al 2013). In addition, the accuracy of the estimated breeding value can be as well increased early in life (Jenko et al 2017). In support, Nguyen et al (2016) noted improved accuracies of selection in both Holstein–Friesian, and Jersey cows having values of 0.39–0.57 and 0.44–0.61 respectively. The consensus is that genetic difference for adaptability exists among cattle (Weller et al 2017). Further genetic variation is obtained through the use of genomic selection, hence increasing the response to selection. Genomic selection enables selection of young bulls and heifers on the basis of their tolerance to heat stress GEBVs (Nguyen et al 2016). More so, the marginal cost of the added GEBV is little since most bulls are already genotyped. Merits of heat tolerance trait include extended animal's longevity thus improving lifetime productivity. However, it was noted that genomics selection does not lower rates of inbreeding in a dairy herd (Silva et al 2014) and predictions in small herds is a challenge due to too small progeny tests.

Final Considerations

Heat tolerance in the present era of improving milk productivity is a trait worth noting due to the associated negative effects of heat stress and increasing production. High-temperature experiences resulting from climate change further intensify the occurrence of heat stress in the dairy herd. In response, cows undergo homeostasis and changes in their physiological state (ie acclimation), so as to alleviate heat stress. Temperature–humidity index has been broadly used in several studies as a heat stress indicator. There is variation in response to heat stress within herds and across regions and this shows that some individual cows are better adapted to high temperatures than others. Regressing the phenotypic performance data as a function of the THI using the Random Regression Model, additive genetic variances can be estimated with high accuracy and flexibility for heat tolerance. Furthermore, heat tolerance level in a dairy herd can be obtained with the use of Hierarchical Bayes Model, which is also noted to be a more realistic method of measuring heat tolerance levels in dairy herds. This review noted that adaptive response to heat stress varied in different dairy herds across regions and this implied that the tolerance level to heat stress differs as well among the dairy herd. Before practicing genetic selection or genomic selection, heat tolerance level assessment is important because it enables identification of cows that have superiority with regards to heat stress yet still producing high milk. Since there is limited research on THI for semi-arid regions under pasture-based, assessing heat tolerance level would have a great impact on the alleviation of the effects of the increase in temperature.

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Conflict of interest

The authors declare no conflict of interest.

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