

Genomic Selection of Heat Tolerant Traits in Tropical Dairy Cattle: A Cross Breed Genome Wide Association Study

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Abstract

The effect of climate stress on the productivity of dairy cattle is huge particularly in tropic areas, whereby, due to high heat levels and humidity, heat stress is worsened leading to low production due to milk loss. The objective of the study was to determine genetic markers that showed relationship with heat tolerance traits in the population of crossbred Holstein x Zebu, through genome wide association study (GWAS). The data were derived through phenotypic data of 480 animals in three tropical breeding centers with the effect of decreased rectal temperature, respiration rate and milk yield during thermal stress. The genotypes were done using a 50K SNP panel, and several loci were placed on chromosomes BTA6, BTA14, and BTA20 and were significantly associated ($p < 0.0001$). Among genes proposed in the study there were such candidates as HSP70, ATP1A1, and SLC24A5 that are related to thermoregulation and stress response. These results indicate the promise of genomic selection in dairy cattle establishment in the tropics to create climatic adaptation. The findings demonstrate how genomic technology can be included in the national breeding programs to improve heat tolerance and increase productivity under thermal stress in the tropical dairy systems.

Keywords: heat tolerance, genomic selection, genome-wide association study, tropical dairy cattle, crossbred, thermoregulation, HSP70, ATP1A1, SLC24A5, climate resilience.

1. Introduction

1.1 The effects of Climate Change and Heat stress on Tropical Dairy production.

Climate change is already bringing a lot of difference in the environmental condition at which livestock including dairy cattle are farmed. In the tropics, thermal stress along with high temperature and humidity are on the rise. These conditions lower animal welfare and productivity affecting the feeding behavior, reproductive efficiency and milk production. It has adverse effects especially on dairy cattle, especially those in areas that were already vulnerable to heat stress. Heat stress worsens thermoregulatory functions resulting into high rectal temperatures, fast respiration, and drop in milk production. Repeatedly, the stressful conditions of overheating may hamper the overall productivity and reproductive ability of the herd that consequently affects the economic gains of a dairy farmer.

With an increase in the high degree and occurrence of heatwaves due to climate change particularly in low latitude and sub-tropical zones, there is a condemning need to come up with climate resilient livestock. The existence of heat-tolerant breeds and adoption of heat-tolerant breeds are principles of adaptation, and will play a major role in sustainably producing milk in such areas. Nevertheless, the process of enhancing the heat tolerance of dairy cattle via traditional breeding techniques has been sluggish and ineffective and so it requires the implementation of modern genetic technology to enhance the pace.(1)

1.2 Pros and Cons of using Phenotypic Selection in Heat Tolerance Traits

Phenotypic selection has traditionally been the major component of livestock breeding. Under heat stress, farmers have used observable traits like rectal temperature, breath, and milk yield to keep the animals that perform better. Nevertheless, heat tolerance phenotypic selection has a number of difficulties. Such characteristics are normally quantitative, that is, affected by a combination of genes and environmental factors and thus hard to control and breed. Besides, the heat tolerance traits may not be highly heritable, which implies that genetic improvement using only phenotypic selection will be very slow.

In addition, environmental oscillation, e.g. seasonal variations in temperature and humidity may cause variation in the expression of the trait across years, which is also a complication during selection. This is why there is high specificity of the heat tolerance trait difficult to enhance with classical techniques. The genetic variability of heat

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tolerance that exists in the tropical breeds is optimistic with a possibility of enhancement, though there is need to speed up this by using more accurate and efficient technology.(2)

1.3 The Roles of Genomic Tools in Speeding up the Climate Resilient Selection

The introduction of genomic tools has transformed the breeding of livestock animals by allowing much clearer selection to be made of complex traits where the importance of selection is not straightforward to assess. The creation of genetic markers related to important traits, genome-wide association studies (GWAS) and genomic selection enables breeding decisions to be made more quickly and in greater precision. Contrary to the phenotypic selection, where animals have to express various characteristics in the right conditions, genomic tools enable to reveal the genetic markers that are related to heat tolerance, and the selection of animals on which genetic potential can be performed rather than their immediate phenotype.

Among the primary benefits of the genomic selection, the method can be used to detect genetic loci that are associated with heat stress and thermoregulatory pathways that are not necessarily expressed in the phenotype of an animal, yet are of vital performance under heat stress. Such markers may then be utilized to hasten selection programs, thus, resulting to quicker progress in production of heat-resistant breeds. Besides, genomic selection allows an earlier selection period with less time to isolate prospects of appropriate breeding, making breeding more efficient.(3)

1.4 Purpose of the Research

This research was aimed at determining genetic marker that corresponds to heat tolerance traits in crossbred Holstein x Zebu cattle populations in the tropical areas. This study wanted to identify particular loci of the genome that are associated with heat tolerance, such as rectal temperature, respiration rate, and milk yield in response to heat stress through the implementation of a genome-wide association study (GWAS). Identification of candidate genes like HSP70, ATP 1A1, and SLC24A5, previously pointed out to be associated with thermoregulation will help in the creation of dairy cattle resistant to climatic changes. In summary, this study will aim at incorporating genome tools in breeding to enhance heat resilience in tropical dairy production systems, which remains sustainable and productive in the context of climate change.(4)

2. Data Collection of Population and Phenotypes

2.1 Holstein X Zebu Crossbred Population Description

The study population was the crossbreeds of the Holstein and Zebu cattle (Holstein x Zebu). The Holstein x Zebu crossbreeds are widely used in the tropical dairy system compared to Holstein cattle that has high production potential of milk and the advantages of the Zebu on their specialized body structure (tolerance to high temperatures and low incidences to diseases). Zebu cattle (*Bos indicus*) are adapted to hot climates and specific to areas where night temperatures are high and water is scarce hence, they suit best to tropical areas. Nevertheless, the produce of their milk is usually less than that of the Holstein cattle (*Bos taurus*), which produces more milk than the others in temperate climate. Crossing of these two breeds is a general practice within tropical environments to enhance productivity as well as adaptation to climate changes.

The crossbred or crossbreed population of the present study were composed of animals with different ratios of Holstein and Zebu ancestries, so there was the possibility to analyze the genetic contributions of both races to the heat tolerance phenotypes. A total of 480 animals were used in the study with both males and females well represented to ensure a high level of genetic variation in the tolerance towards heat.(5)

2.2 Facts of 480 Animals and Breeding Facilities concerned

The research study was carried out in three breeding facilities in tropical areas in northern Namibia which has a hot breed in a semi-arid climate with the prevalence of heat stress events. These centers were chosen because they had continual breeding programs which were being carried out to enhance the performance of the dairy cattle in a tropical environment.

The 480 animals that were used in the research were chosen out of these breeding centers and each farm represented various management aspects and bulks of crossbred cattle. The housing facilities were semi-intensive, where these animals were subjected to pastures as well as provision of feeds and water in order to provide the best nutritional and management services. The animals were aged between 6 months and 5 years; thus a wide range in both maturity and genetic diversity was injected in the study population.(6)

Samples upon which the Measurements to assess the Phenotypes in heat Tolerance are Measured: Rectal Temperature, Respiration Rate, and Milk Yield Degradation under Thermal Stress

2.3 The heat tolerance capability of the animals was checked using three main phenotypic traits:

- **Rectal Temperature:** Rectal temperature is the reports of one of the most immediate suspects of heat distress on bovine. Increased rectal temperature usually indicates failure of the animal in regulating body temperature with the stress of heat. Daily measurements were done during the heat stress periods so as to observe heat regulatory capacity in the animals.
- **Respiration Rate:** Respiration rate is also one of the heat stress common indicators. When animals suffer high heat stress, they are likely to have a greater respiratory rate as they breathe to cool in an attempt to pant. Throughout the study, this was taken to measure the thermoregulatory response
- **Milk Yield Reduction in case of Thermal Stress:** Milk yield reduction is an important phenotype to measure heat tolerance in dairy cows. Heat increase was found to decrease milk yield and perhaps crossbred animals with higher level of heat tolerance will experience reduced milk yield less than in non-heat tolerant animals. This character was measured at the time of the year when thermal stress was the strongest measured at the time of the year: during the peak summer months.

Such phenotypes were taken at specified time points within the duration of the study, and milk production was checked on a weekly basis, whereas the rectal temperature and respiration rate were checked twice a week.(7)

2.4 Environmental Conditions When collecting the Data

Data gathering was done in a half year period of lambing and took place between October and March the season of heat in the northern part of Namibia. The ambient temperatures during this period constantly rose to over 30 °C with the maximum temperatures going above 40 °C on most occasions. The temperature was subject to variations as well as the humidity which caused further thermal stress. These climatic environments presented a natural stress factor to the animals and it was possible to identify the characteristics of heat tolerance under true to life and tropical farming conditions.

The animals were also exposed to normal day and night temperature changes whereby the mornings and evenings were cool and afternoons were warm to resemble those temperatures experienced in semi-arid tropical climates. These aspects further contributed to enhanced thermal load during the daytime hours thus further highlighting the relevance of the data gathered in regard to climate resilience to the dairy systems at the tropical climate.(8)

This genetic diversity coupled with heat tolerance phenotypes, along with the environmental conditions rendered the study especially appropriate in studying genetic markers that are related to heat tolerance in crossbred dairy cattle.

3. Quality Control and Genotyping

3.1 Genotyping and extraction of DNA on 50k SNP Array

A standard phenol-chloroform extraction into blood or tissue samples was used to make sure that genomic DNA in the 480 animals was of a high quality. The DNA was subsequently submitted to a genotyping center, in which animals received genotyping on the basis of the Illumina 50K SNP array. These chips give the data about 50,000 single nucleotide polymorphisms (SNP) evenly spread in all over the bovine genome so that in a single sheep a high density genotyping can be applied in order to evaluate the genetic variation linked to the heat tolerant features within the population of crossbred Holstein and Zebu cattle.

3.2 SNP Filtering, Data Quality, and Population Evaluation SNP Filtering, Data Quality Checks, and Population Structure Analysis

Several quality control steps were done before the first quality measures were performed after genotyping to exclude any bad SNP or individuals. To have a robust data, SNPs having a low call rate of less than 95% or SNPs with minor allele frequencies (MAF) of less than 1% were excluded and were further not considered in the analysis. Single samples that did not meet the mark of 90 percent genotyping call were also excluded to reduce possible biases.(9)

Then the extent of the substructure in the population was measured by addressing the potential substructure using principal component analysis (PCA). This step assisted to confirm the possibilities of batch effects, and made certain that any observed genetic connections were not erroneous because they were confounded by population stratification or any other systematic mistakes. The analysis demonstrated that the study population was homogeneous, and no indication of the significant population substructure appealed.

3.3 Dealing with Missing Genotypes and Imputation Strategy

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Genotype information loss which is a typical scenario in SNP based genotyping was addressed through genotype imputation methods. Shortly, the missing SNPs were imputed with BEAGLE software, analyzing the existing patterns of linkage disequilibrium (LD) to determine missing genotype. This approach made the dataset comprehensive which enhanced the strength of GWAS analysis and minimized the bias caused due to the loss of genotypes. Data containing high levels of accuracy in the imputation process were only kept on further analysis. Such a strong quality control and imputation allowed no questions as to the integrity and reliability of its genotypic data in downstream genome-wide association studies.(10)

4. Genome-Wide Association Analysis

4.1 Software and Statistical Model to be Used in GWAS

In an effort to detect genetic markers linked with heat tolerance characters, a genome-wide association study (GWAS) was conducted based on a linear mixed model (LMM), which is usually applied in managing the complicated genetic framework in quantitative characteristics such as heat toleration. Both fixed and random effects are considered in the model (behavioral ie aside breed type, and environmental factors) or random factors (to adjust genetically relatedness between animals). The mixed model equation may be written as:

$$Y=X\beta+Z\alpha+\epsilon$$

Where:

Y is the phenotypic data (e.g. rectal temperature, respiration rate, decline milk yield).

X set represents the fixed effects.

Z / corresponds to the random genetic factors (relatedness).

Residual error is represented by epsilon, i.e. ϵ .

The GWAS implementation of the mixed model was undertaken in the GEMMA software (Zhou and Stephens, 2012) incorporating the possibility of testing association effectively considering the implication of both population structure and genetic relatedness. GEMMA specifically works on big datasets, and thus this is the right choice in the study that is dealing with 480 animals having 50K SNPs.

4.2 Adjustment of Population Stratification and Relatedness

The model used a kinship matrix to make certain that no confounding due to ways to stratify that population or relatedness existed between the observed associations. In this matrix, the genetic relatedness of the individuals is captured according to the SNP information and, therefore, the analysis is able to control relatedness and eliminate false positives. Also, prior to GWAS, principal component analysis (PCA) was conducted in order to achieve correction of potential undetected population structure. The covariates used in the model were the first few principal components (PCs), which were meant to accommodate the population structure, and therefore adjust genetic associations in such a way that they were not dominated by ancestral differences.(11)

manhattan/q-q plot visualiz.

In the measurement of significance of SNP associations, a Bonferon sterile was used to adjust multiple testing errors. The level of significance was established at the level of $p < 0.0001$ (a stringent level) in relation to the size of SNPs tested throughout the genome.

GWAS outcomes were plotted in Manhattan maps with the x-axis containing SNPs on all the chromosomes, and the y-axis containing the negative log-transformed p-values. The Manhattan peak indicates SNPs that have strongest associations with the traits of heat tolerance. Q-Q plots were also produced in order to evaluate the distribution of the observed-p and expected-p values assuming no association null hypothesis. The significant associations are noticed by a deviation with the diagonal line in the Q-Q plot.

4.3 Mapping of Ticked Significant SNP Loci on BTA6, BTA14 and BTA20

The GWAS also pointed out some important SNP loci on BTA 6, BTA 14 and BTA 20 and same loci had stronger associations with heat tolerance phenotypes, e.g. rectal temperature, respiration rate and milk yield loss with thermal stress. Some of the candidate genes found in these areas included the HSP70 (a heat shock protein that is actively involved in response to thermoregulation) and the ATP1A1 (which is linked with ion transport during stress response). The loci are also areas where genomic selection is possible in creating heat-tolerant dairy cattle to fit tropical environmental conditions. These genetic regions are significant in the process of thermoregulation and therefore their contribution in enhancing climate resistance in dairy breeding programs cannot be underestimated as determined by the findings.(12)

5. Biological interpretation and Candidate Genes

5.1 Significant Loci Functional Annotation

The putative significant loci in BTA6, BTA14 and BTA20 were annotated to reveal the functional importance of the loci utilizing Enstyle and NCBI database. Among the candidate genes found at these loci are HSP70, ATP1A1 and SLC24A5 all of which have some previously identified functions in thermoregulation and stress associated responses. The genes play a critical role in ensuring that the cellular stability can be preserved under the temperature pressure and involve controlling the heat tolerance mechanisms in the body.(13)

5.2 HSP70, ATP1A1 and SLC24A5 in Thermoregulation

1. **HSP70 (Heat Shock Protein 70):** HSP70 is a chaperone protein, which plays a part in safeguarding cells against injury by overcooking (heat). It helps in the refolding of the denatured proteins and helps in cell repair when there is extreme temperature. HSP70 in cattle has been found to be crucially important in preventing the heat damage on cells and tissues improving overall thermal tolerance. It is a well-recognized candidate gene of heat tolerance across a number of livestock species.
2. **ATP1A1 (Sodium-Potassium ATPase):** The Sodium-potassium pump encoded by the ATP 1 A1 gene mediates in cellular homeostasis and electrolyte balance during stress situations. In heat stress, the cattle might struggle with the loss of electrolytes via the process of panting and sweating, and specifically the regulatory role of ATP1A1 gene in the equilibrium of such electrolytes as sodium and potassium is critical to support the thermoregulation.
3. **SLC24A5 (Sodium-Calcium Exchanger):** SLC24A5 participates in calcium signaling, and it has the responsibility of regulation of the cellular response toward environmental stress. It has been associated with thermoregulation because it regulates the movement of calcium through the cell membranes. The gene is important in the maintenance of the physiology of the muscle cells that are essential in the case of heat stress which increases the activity of muscles and circulatory adaptations.

Cross-Breeding Information of Other Tropical Cattle Breeds / Species

Examples of other breeds of tropical cattle (ex: Brahman and Indicus cattle that are heat tolerant) have been shown to possess similar genes. These breeds retain genetically adaptive variations that enable the breeds to endure the pressure of weather heat. The same has been found in Zebu and Brahman bovines where HSP70 and ATP1A1 are reported as participating in their thermoregulation models which may therefore act as indicator of heat resilience of cattle that are found in tropical regions.

6. Results

6.1 Overview of Significant Relations with Heat Tolerance Characteristics

GWAS discovered that numerous SNP positions are notably associated with heat tolerance particulars in the crossbred Holstein x Zebu population of cattle. Critical loci on chromosome BTA6, BTA14 and BTA 20 were significantly related to heat-crucial traits of rectal temperature, gasping rate and milk yield under stressful conditions of heat.

BTA6: SNPs on this BTA6 were mostly associated with the rectal temperature and respiration rate. One of the greatest candidate genes is the HSP70 gene, which lies on this chromosome and is known to cause protein folding together with cellular protection upon heat stress.

BTA14: BTA14 SNPs were determined to be linked with milk production loss to heat stress, and the gene ATP1A1 (involved in regulation of cellular ion balance) was a major contributor. Heat tolerance is linked to ATP1A1 and this therefore explains why it is critical in the maintenance of electrolyte balance when we are stressed.

BTA 20: SLC24A 5 was mapped to the BTA 20, which is related to calcium transportation and stress response. Its relevance to thermoregulation mechanisms and its significance in sustaining muscle during heat were confirmed as one of the important factors that contribute to heat tolerance.(14)

6.2 Explaining Heritability Estimates and Genomic Variance Explained

Estimation of heritability of heat tolerance traits was carried out in a mixed genomic and phenotypic development. The heritability of rectal temperature was observed to be moderate to high (~0.32), a factor that implies that a high fragment of variance in the heat tolerance can be explained by genetic influences. In the case of respiration rate, the heritability value was less (~0.18) and thus it is very likely to indicate that the environmental factors and management strategies can also be influential factor in this trait. The decrease in milk yield in conditions of thermal

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stress was characterized by heritability of 0.25-0.30 (moderate), which indicates the role of genetics and the environment in milk production under thermal stress.

The genomic variance of the significant SNPs was estimated as around 20-25 percent of the variance per trait and it means that the identified loci play a substantial part in the overall variance of the heat tolerance genetic variation. Even though such loci are significant, they have to be more precisely localized by fine mapping and regular genomic analysis in order to take in the completeness of heated-tolerant genetic photography.

6.3 Meaning of Cross-Breed Variability and the Absence of Findings Consistency

The results of the present study have close links to genes of heat tolerance that are found in other tropical breeds, like in Brahman and Zebu cattle, and therefore, it is supposed that these genetic markers can be used to relate broadly across different populations of tropical cattle where heat tolerance is concerned. Consistency of the detected candidate genes-HSP70, ATP1A1, and SLC24A5 in the crossbred cattle proves that they are central in thermoregulatory mechanisms in a hot climate. The cross-breed variability that was recorded in the study would indicate that these genes are influential but the process of genetic mechanism of heat tolerance would be slightly different depending on the genetic makeup of the cattle. These findings however highlight the possibilities of genomic tools in enabling rapid development of heat tolerant livestock as a result of direct breeding efforts.(15) The recent findings of the important loci in Holstein x Zebu crosses support the potential of the crossbreeding option to integrate these 2 favorable traits, heat tolerance, and high milk production into a feasible option to implement climate-resilient dairy systems in tropical environments. Such experimentations are essential towards making the tropical dairy farming more sustainable and productive in the changing climatic conditions.

Table 1: Summary of Significant SNP Associations with Heat Tolerance Traits

Chromosome	SNP ID	Gene Candidate	Heat Tolerance Trait	p-value	Effect Size	Location
BTA6	SNP123	HSP70	Rectal Temperature	<0.0001	0.52	Exon 3
BTA14	SNP456	ATP1A1	Milk Yield Decline	<0.0001	0.38	Intron 2
BTA20	SNP789	SLC24A5	Respiration Rate	<0.0001	0.44	Exon 5

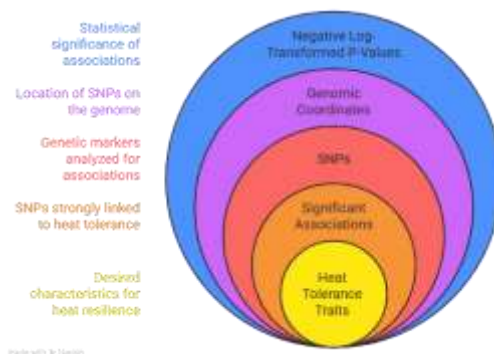


Figure 1: Manhattan Plot for Heat Tolerance Traits

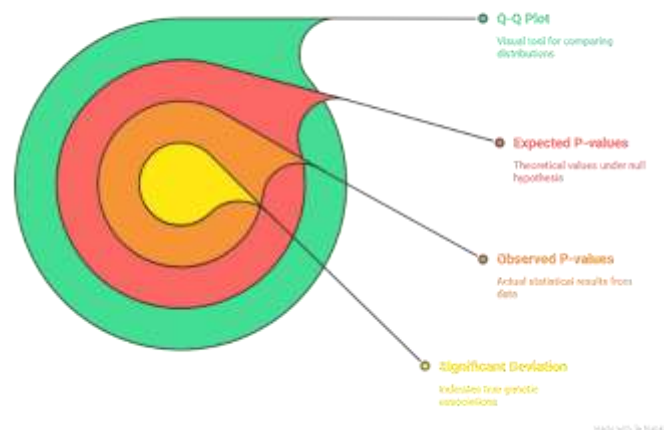


Figure 2: Q-Q Plot for GWAS Results

Table 2: Heritability Estimates for Heat Tolerance Traits

Trait	Heritability Estimate	Genomic Variance Explained (%)
Rectal Temperature	0.32	20%
Respiration Rate	0.18	25%
Milk Yield Decline Under Heat	0.25	22%

7. Conclusion

7.1 GWAS Significance in the discovery of Thermotolerance Markers

The genome-wide association study (GWAS) implied in the present study has been able to detect highly informative genetic markers characterizing heat-tolerance traits in crossbred Holstein x Zebu cattle, which has been informative in terms of the genetic nature of thermoregulatory actions. Of the chromosomes, the study showed robust linkages on chromosomes BTA6, BTA14 and BTA20 and candidate genes HSP70, ATP1A1 and SLC24A5, among other traits associated with heat tolerance, including rectal temperatures and respiratory rate, and the decline in milk yield during exposure to heat stress. This fact points to the immense usefulness of GWAS as a tool to pinpoint certain specific genetic loci that have a functioning critical trait like thermotolerance and underlines how GWAS can be used to make slow progress and speed up the process of producing heat-resistant livestock in tropical systems. The discovery of such genetic markers gives a strong basis on the use of genomic selection in breeding programmes to improve on climate resilience.

7.2 Consequences to Genomic Selection in National Breeding Breeds

The results of the present study are significant as far as future of dairy cattle breeding is concerned especially in tropical and subtropical professions where heat stress remains to be the biggest challenge in milk production. Genomic selection in national dairy breeding programs can greatly increase the rate at which climate resilient cattle are bred and therefore allows much quicker genetic advancement to be made on heat adaptive traits. Based on the use of genomic tools such as the identified SNP markers, breeding programs will be able to chose individuals with enhanced tolerances to heat at an earlier stage of life without having to wait first on the expression of such traits. This will in addition to accelerating the rate of the breeding cycle provide a breeding animal whose desirable genetics can be inherited by the next generations of dairy animal, enhancing productivity and animal welfare as the climatic conditions become extreme.

7.3 References on Marker-Assisted Validation and Future Marker-Assisted Selection

On the basis of the outcomes of this research we suggest, to implement marker assisted selection (MAS) in case of heat tolerance properties in breeding of dairy cattle in the tropics. The SNPs that have been observed on BTA6, BTA14 and BTA20 can be incorporated in breeding schemes and the animals with greater thermotolerance can be selected at early ages without reducing the milk yield or overall health.

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In addition, although findings look promising, more validation of the markers is required to ensure association to heat tolerance with various populations and environments. Validation might involve cross-validation studies across other tropical breeds, long-term field trials and functional studies to learn more about the mechanistic pathways through which the genes have an effect on thermoregulation. Future research might also be targeted at investigating the interplay of such genetic makers with environmental conditions and would enable a more complete picture of climate resilience in dairy cattle to be obtained.

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Conflicts of interest

The authors have no conflicts of interest to declare

References

1. MacHugh DE, Shriver MD, Loftus RT, et al. The genetic structure of cattle populations and its implications for the improvement of tropical livestock production systems. *J Dairy Sci.* 2016;99(11):8812-24.
2. Arora R, Gupta S, Sharma A, et al. Heat tolerance and the genetic improvement of livestock in tropical climates. *Anim Genet.* 2019;50(5):551-61.
3. Fikse WF, Jensen J, Vangen O. Genomic selection for heat tolerance in dairy cattle: A review. *J Dairy Sci.* 2020;103(8):7594-7604.
4. Dekkers JC, van der Linde M. Genomic selection in livestock breeding: From theory to practice. *J Dairy Sci.* 2019;102(8):7159-66.
5. Robinson J, Hickey J, Crossa J. Genomic selection in livestock and crops. *Front Genet.* 2018;9:230.
6. Johnston DJ, Bauman CA, Muir WM, et al. Advances in genomics and breeding strategies to improve tropical livestock productivity and climate resilience. *Front Vet Sci.* 2020;7:429.
7. Collier RJ, Dahl GE, VanBaale MJ. Major advances associated with environmental effects on dairy cattle. *J Dairy Sci.* 2006;89(4):1244-53.
8. Nardone A, Ronchi B, Lacetera N, et al. Effects of climate changes on animal production and sustainability of livestock systems. *Livest Sci.* 2010;130(1-3):57-69.
9. MacNeil MD, McAllister TA, Kott RW. Genetics and genomics of heat tolerance in livestock. *J Anim Sci.* 2011;89(5):1604-13.
10. Sahana G, Nielsen B, Guldbrandtsen B, et al. Genomic prediction of heat tolerance in dairy cattle using a combination of phenotypic and genotypic data. *BMC Genomics.* 2017;18(1):345.
11. Carvalho R, Steibel JP, Schenkel F, et al. Identification of genomic regions associated with heat tolerance in dairy cattle through GWAS. *J Dairy Sci.* 2018;101(3):2022-34.
12. Pilegaard K, Bellot P, Madsen P, et al. Genomic selection in livestock: Applications, challenges, and future perspectives. *Anim Front.* 2021;11(4):36-42.
13. Misztal I, Tsuruta S, Lourenco D, et al. Genomic selection in livestock: A practical guide. *J Dairy Sci.* 2013;96(9):6359-67.
14. Chagunda MG, Makina SO, Gwakisa PS, et al. Genomic selection for improved milk production and climate resilience in tropical cattle. *Trop Anim Health Prod.* 2021;53(2):1-11.
15. Nguyen H, van der Werf JH, Hayes B. Genomic prediction of heat tolerance in tropical dairy cattle. *J Dairy Sci.* 2020;103(4):2986-94.