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ABSTRACT

Climate change-induced rise in global temperatures has intensified heat stress on dairy cattle and is contributing to the generally observed low milk productivity. Selective breeding aimed at enhancing animals' ability to withstand rising temperatures while maintaining optimal performance is crucial for ensuring future access to dairy products. However, phenotypic indicators of heat tolerance are yet to be effectively factored into the objectives of most selective breeding programs. This study investigated the response of milk production to changing heat load as an indication of heat tolerance and the influence of calving season on this response in multibreed dairy cattle performing in three agroecological zones Kenya. First-parity 7-day average milk yield (65 261 milk records) of 1 739 cows were analyzed. Based on routinely recorded weather data that were accessible online, the Temperature-Humidity Index (**THI**) was calculated and used as a measure of heat load. THI measurements used represented averages of the same 7-day periods corresponding to each 7-day average milk record. Random regression models, including reaction norm functions, were fitted to derive two resilience indicators: slope of the reaction norm (Slope) and its absolute value (Absolute), reflecting changes in milk yield in response to the varying heat loads (THI 50 and THI 80). The genetic parameters of these indicators were estimated, and their associations with average test-day milk yield were examined. There were no substantial differences in the pattern of milk yield response to heat load between cows calving in dry and wet seasons. Animals with ≤50% *Bos taurus* genes were the most thermotolerant at extremely high heat load levels. Animals performing in semi-arid environments exhibited the highest heat tolerance capacity. Heritability estimates for these indicators ranged from 0.06 to 0.33 and were mostly significantly different from zero ($P < 0.05$). Slope at THI 80 had high (0.64–0.71) negative correlations with average daily milk yield, revealing that high-producing cows are more vulnerable to heat stress and vice versa. A high (0.63–0.74) positive correlation was observed between Absolute and average milk yield at THI 80. This implied that low milk-producing cows have a more stable milk production under heat-stress conditions and vice versa. The study demonstrated that the slope of the reaction norms and its absolute value can effectively measure the resilience of crossbred dairy cattle to varying heat load conditions. The implications of these findings are valuable in improving the heat tolerance of livestock species through genetic selection.

Implications

The global increase in ambient temperature necessitates the need to incorporate heat tolerance in dairy cattle breeding objectives. Reaction norm functions can be used to express heat tolerance as a phenotypic response of animal performance to a changing heat load environment. The slope of this reaction norm and its absolute value are heritable and can be utilized as indicators of tolerance to heat stress. An antagonistic correlation exists between heat tolerance and milk production in dairy cattle. Therefore, combining milk production potential with heat tolerance in a multitrait selection index could help improve dairy productivity.

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Introduction

Climate change has caused global atmospheric temperatures to rise by more than 1.5 °C in the past few decades (IPCC, 2014, 2022). The high temperatures are accompanied by varying magnitudes of heat waves, erratic rainfall patterns, and frequent and prolonged droughts, depending on the geographical zone of the world (Nardone et al., 2010; Rojas-Downing et al., 2017). Increased variability in ambient temperatures is predicted to occur in tropical countries in the near future (Bathiany et al., 2018). These changes have far-reaching detrimental consequences on livestock production depending on the livestock species kept and the production type adopted (Thornton et al., 2009; Henry et al., 2012, 2018), especially in low-income countries. Despite an already observed low dairy production in sub-Saharan Africa (**SSA**), the ongoing climate change threatens to slow and even halt any progress that has been made in increasing productivity. This is likely to reduce food availability, render people jobless, and increase the frequency and severity of human diseases (Thornton et al., 2009).

In SSA where a larger proportion of dairy production comes from resource-poor farmers, high temperatures and prolonged droughts due to climate change have reduced the amount of water and feed resources available for dairy herds and increased the vulnerability of animals to emerging diseases (Thornton et al., 2009; Nardone et al., 2010; Rojas-Downing et al., 2017). Elevated ambient temperature results in heat stress in animals, which reduces milk production, growth rates, reproductive performance, welfare, and health of the dairy cattle (Nardone et al., 2010; Rojas-Downing et al., 2017; Hernández-Castellano et al., 2019). Whereas enhanced herd management and animal husbandry practices such as the provision of sheds and ad libitum water supply can alleviate the effect of heat stress on animals, it is short-term and not sustainable in the long run (Oloo et al., 2023b; Ekine-Dzivenu et al., 2022; Oloo et al., 2022a). There is therefore, a growing need to address the detrimental effects of heat stress on dairy cattle and develop long-term sustainable strategies to mitigate the problem.

Selective breeding for enhanced animal resilience to environmental disturbances may offer a long-term solution for addressing the impact of climate change on livestock species (Shields and Orme-Evans, 2015; Weindl et al., 2015; Berghof et al., 2019). Indeed, cattle differ in heat tolerance capacity and the Zebu breeds are known to exhibit higher thermotolerance capacity (Hansen, 2004; Renaudeau et al., 2012; Mwai et al., 2015; Kim et al., 2017). Previous studies have reported significant heritability estimates (0.13–0.19) for the body (Mateescu et al., 2022) or rectal (Dikmen et al., 2012; Riley et al., 2012) temperatures under high heat conditions as proxies for heat tolerance in beef and dairy cattle. Underlying genomic regions and/or candidate genes that confer better tolerance to heat stress in cattle have been identified (Macciotta et al., 2017; Srikanth et al., 2017; Sigdel et al., 2019; Cheruiyot et al., 2021). This implies that genetic improvement of thermotolerance in cattle is possible through genetic and marker-assisted selection. Although genomic selection is the most effective method, the high cost of genotyping animals across populations has impeded its wider application in developing countries (Mrode et al., 2019).

Recent studies have shown promising prospects for utilizing genotype by environment interaction (GxE) in estimating resilience-related phenotypes for animal production traits (Hayes et al., 2003; Mulder, 2016; Shi et al., 2021). Individual phenotypes are described as a continuous function of an environmental variable using random regression models (Martin et al., 2011). Reaction norm functions are then used to express resilience as a phenotypic response of animal performance to a changing environment. The slope of the reaction norm shows the environmental sensitivity of a genotype with slope estimates that significantly differ from zero, interpreted as significant G x E. Individuals with a flat slope are said to be environment-sensitive or robust (Streit et al., 2012, 2013; Schmid et al., 2021). As such, the slope estimate in adverse environmental conditions can be used to determine genotypes that are resilient to the challenging state of affairs.

Berghof et al. (2019) proposed the slope of the reaction norm to be an indication of resilience toward a macro-environmental disturbance, such as heat stress. Consequently, the response of milk yield to varying heat loads has been investigated as a potential indicator of thermotolerance in sheep (Sánchez-Molano et al., 2020; Tsartsianidou et al., 2021) and goats (Sánchez-Molano et al., 2019). The phenotypes derived in the previous studies had significant genetic variation and were informative about the resilience to weather variability. The study by Tsartsianidou et al. (2021) reported a significant contribution of season of lambing in the adaptation of sheep to fluctuating heat loads and recommended its inclusion in selective breeding programs.

However, the resilience phenotypes based on the response of milk yield to varying heat loads have not been examined in dairy cows performing in African tropics. The objectives of this study were to (i) depict the shape of the response of milk yield to heat stress for different cattle populations performing in SSA, (ii) derive resilience phenotypes based on milk production changes in response to fluctuating heat loads, (iii) determine the impact of the season of calving on the resilience of animals to heat stress, and (iv) investigate the genetic parameters of these resilience phenotypes.

Material and methods

Data

First parity 7-day average milk yield records of cows of different breeds that calved between 2001 and 2021 from three different herds performing in different agroecological zones of Kenya were used in this study. Two of the herds were performing in the agroecological zone IV (semi-arid) but in regions of the country where different agricultural practices were predominant. The agricultural practices adopted in the region were thus used to classify the farms as semi-arid arable (**SAA**) and semi-arid pasture-based (**SAP**). The third farm was in agroecological zone V (semi-humid (**SH**)). The climatic conditions of these agroecological zones and breeding practices adopted in each farm were described by Oloo et al. (2023a). Data were edited to exclude milk yield values that deviated by more than four SD from the mean and animals with less than three records in a whole lactation. To correct for season and year of calving, contemporary groupings of year-season (**YS**) were defined. Each agroecological zone had four seasons that were based on the precipitation pattern, as previously described (Oloo et al., 2023a). Long and short rain periods were considered wet seasons 1 and 2, respectively. A dry period before the long rain was considered as dry season 1 and that before the short rains as dry season 2. Any YS group with less than three records was excluded from the analysis. The final dataset consisted of 65 261 7-day average milk records (hereafter referred to as daily milk yield records) from 1 739 animals. The animals were grouped into three breed groups based on the proportion of taurine genetics in their breed composition: breed group (1) (**BG1**) ($\leq$ 50% *Bos taurus*, n = 689), **BG2** (> 50–87.5% *Bos taurus*, n = 450), and **BG3** (> 87.5–100% *Bos taurus*, n = 600).

Weather data of each farm were obtained from the NASA POWER (National Aeronautics and Space Administration (NASA) Langley Research Center (LaRC) Prediction of Worldwide Energy Resource (POWER) Project funded through the NASA Earth Science/Applied Science Program based on their GPS coordinates.

The data included average daily temperature and relative humidity, which were used to calculate daily temperature-humidity index (**THI**) using the formula of the National Research Council, (1971) as follows:

$$THI = (1.8 \times T_{ave} + 32) - [(0.55 - 0.0055 \times RH_{ave}) \times (1.8 \times T_{ave} - 26.8)] \quad (1)$$

where T_{ave} and RH_{ave} are average temperature and relative humidity, respectively. THI for each test-day was computed by averaging the average daily temperature and relative humidity data over the test-day and 3 days preceding it. This extended timeframe allowed for the determination of the prolonged effects of heat stress on milk production on a given day (Bohmanova et al., 2007; Hammami et al., 2013, Ekine-Dzivenu et al., 2020). The calculated THI measurements within the same 7-day periods were averaged to correspond with each 7-day average milk record for every animal.

Population-level reaction norms

The following random regression model, including reaction norm functions, was fitted to determine population-level changes in milk yield in response to varying heat load.

$$Y_{ijkl} = X + f(\beta, X_j) + a_i + ysm_k + e_{ijkl} \quad (2)$$

where Y_{ijkl} corresponds to the average daily milk yield of i^{th} individual animal under THI j, X corresponds to a set of fixed effects on daily milk yield, $f(\beta,X_j)$ represents the population reaction norm function describing the relationship between the average animal performance and THI j, ai represents the effect of i^{th} individual animal, ysm_k represents random effects of the year-season of milking, and eikjl corresponds to the residual. Reaction norm function was fitted using a Legendre polynomial of the second degree. The choice of Legendre polynomial of order 2 was based on a preliminary analysis that examined orders 1 to 3 to discover which one gave the best fit using Akaike information criterium and likelihood ratio test. The fixed effects adjusted for included: herd, breed, age at calving, year of calving, season of calving, and weeks in milk.

The population reaction norm model was first fitted for the full dataset to determine the general shape of milk yield to changing heat loads for the entire population. The data were also divided into different subsets, as presented in Table 1. The population reaction norm model was then fitted for each subset to depict the populational differences in the shape of the response of milk yield to heat load for different seasons, environments, and breed groups.

Individual resilience phenotypes

The random regression model below was fitted to derive resilience indicators reflecting changes in milk yield in response to varying heat loads.

$$Y_{ijkl} = X + f(\beta, Xj) + f_i(a_i, X_j) + ysm_k + e_{ikjl} \quad (3)$$

where $f_i(a_i,X_j)$ corresponds to the individual animal reaction (expressed as a deviation from the population reaction norm) describing the relationship between individual animal i and THI j. All other terms were as in Eq. (2) above. Similar to Eq. (2), the reaction norm functions were fitted using a Legendre polynomial of second degree.

Individual animal's changes in milk yield in response to heat load were analyzed in two different ways. In the first method, the model described in Eq. (3) was fitted to the full dataset, and all significant fixed effects were fitted. The second analysis aimed at determining the impact of the season of first calving on the resilience of animals to heat stress. The dataset was divided into two seasons of calving subgroups: wet season (29 360 milk records from 780 animals) and dry season (35 901 milk records from 959 animals) and a random model in Eq. (3) was fitted for each group. From the analyses, every animal had two different reaction norms, one based on the entire population, and the other on the season it first calved.

The slope of the individual reaction norm and its absolute value were considered as an animal's resilience phenotypes for heat stress. The slope of the individual reaction norm was determined as the relative steepness of change in the response of each animal's milk yield to heat load at a given THI level. It was estimated as the derivative corresponding to a certain THI on the individual's response curve. For instance, resilience phenotypes would describe a change in milk yield by one THI change at a certain THI level. The reference THI was set to THI 50 and THI 80 to represent distinct resilience traits under no-stress and heat-stress conditions, respectively. These values were derived from the THI level that marked the onset of heat stress at the population level in each farm. Heat stress is triggered at the THI level where the slope of the reaction norm is zero before the beginning of a declining trend in milk yield. The cows in a semi-arid pastured-based environment entered heat stress at the lowest heat load level (THI 52) while those in semi-humid environment entered at the highest heat load (THI 76). Thus, at THI 50, all animals in each farm were ideally not experiencing heat stress and at THI 80, all the animals under the study were heat stressed. The distribution of the absolute value of slopes was normalized by applying a square root transformation.

Table 1
Descriptive statistics of 7-day average milk yield and 7-day average temperature-humidity index (THI) (mean and SD in parentheses) for the entire cattle population, as well as the dry and wet season of calving.

Variable	Number of cows	Number of records	Mean (SD) MY	Mean (SD) THI	Min THI	Max THI
Population	1 739	65 261	9.087 (4.245)	68.09 (6.5)	54.19	81.6
Calving Season						
Dry	959	35 901	9.501 (4.136)	68.85 (6.03)	54.19	81.6
Wet	780	29 360	8.581(4.321)	67.16 (6.93)	54.19	81.6
Environment						
SAA	499	19 391	5.585 (3.597)	59.88 (1.83)	54.19	65.73
SH	398	13 993	12.65 (4.036)	77.43 (1.92)	71.81	81.6
SAP	842	31 877	9.653 (2.917)	68.98 (1.69)	64.45	73.77
Breed group (BG)						
BG1	689	25 282	6.857 (3.982)	64.26 (6.45)	54.19	81.6
BG2	450	17 216	10.989 (3.925)	72.54 (5.3)	54.84	81.6
BG3	600	22 763	10.126 (3.613)	68.98 (4.67)	54.19	81.38

SAP = Semi-arid pasture-based agroecological zone; SH = Semi-humid agroecological zone; SAA = Semi-arid arable agroecological zone. BG1 = ≤ 50% *Bos taurus*; BG2 = > 50–87.5% *B. taurus*; BG3 = > 87.5–100% *B. taurus*.

Fixed effects factors of variation

A fixed effect linear model shown in Eq. (4) was fitted to determine the effect of breed and environment on each resilience phenotype.

$$y_{ijklmno} = A\mu + \text{breed}_i + \text{env}_j + \text{yc}_k + \text{sc}_l + \text{age}_m + \text{Obs}_n + e_{ijklmno} \quad (4)$$

where $y_{ijklmno}$ is the vector for individual resilience indicator measurement for o^{th} animal, μ corresponds to the population mean, breed_i is the i^{th} breed group (i = 1–3), env_j is the environment which combines climatic conditions and herd management (j = 1–3), yc_k is the k^{th} year of calving (k = 1–21), sc_l represents the l^{th} season of calving (l = 2), age_m, represent a linear covariate of m^{th} age at first calving ranging from 21 to 60 months, Obs_n is the n^{th} number of milk records used to calculate the resilient indicator (n = 3–58), and $e_{ijklmno}$ is the residual error. Least-square means (LSM) of different breed groups and environments were calculated and contrasted.

Genetic parameters of resilience indicators

The univariate animal model shown below was used to estimate (co)variance of all the resilience indicators and average daily milk yield using ASReml-R 4.1 (Butler et al., 2017):

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Za} + \boldsymbol{e} \quad (5)$$

where $\boldsymbol{y}$ is a measurement of individual phenotype for the resilience trait, $\boldsymbol{\beta}$ is the solutions of the fixed effects in the model which included breed, environment (which accounted for the confounded effects such as herd management practices), year and season of calving, age at calving, and the total number of average daily milk records; **a** is the solutions of random animal additive genetic effects and $\boldsymbol{e}$ is the vector of random residual effects. The vectors of random animal effects $\boldsymbol{a}$ and residual effects $\boldsymbol{e}$ were assumed to be normally distributed with $\boldsymbol{a} \sim N(0; \boldsymbol{A}\sigma_a^2)$ and $\boldsymbol{e} \sim N(0; \mathbf{I}\sigma_e^2)$, where **A** corresponds to the numerator relationship matrix, **I** correspond to the identity matrix, σ_a^2 is the additive genetic variance, and σ_e^2 is the residual variance. **X** is the incidence matrix relating observations to fixed effects; **Z** is the incidence matrix relating records to random animal effects. The pedigree used to construct the numerator relationship matrix comprised 3 601 animals spanning 20 generations, including 543 sires and 1 927 dams.

The likelihood ratio test was used to test whether the heritability estimates differed significantly from zero by comparing the log-likelihoods of the tested model against a model without random animal genetic effects.

Phenotypic and genetic correlations between the different resilience indicators, and between the resilience indicators and average daily milk yield, were estimated using variances and covariances estimated from the following bivariate mixed animal model:

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix} \quad (6)$$

where y_i is a vector with observations on trait i; b_i is a vector with the fixed effects for trait i, which were the same as in the univariate analysis; a_i is a vector with the additive genetic effects for trait i; and e_i is a vector with the residuals for trait i; X_i and Z_i are incidence matrices linking the records in y_i to the fixed effects and additive genetic effects, respectively. The additive genetic effects for all traits were assumed to follow a normal distribution with a mean of 0, a genetic variance of $\sigma_{a_i}^2$ for trait i, and a genetic covariance of $\boldsymbol{\sigma}_{\boldsymbol{a}_1\boldsymbol{a}_2}$: $\begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \boldsymbol{A} \otimes \begin{bmatrix} \boldsymbol{\sigma}_{\boldsymbol{a}_1}^2 & \boldsymbol{\sigma}_{\boldsymbol{a}_1\boldsymbol{a}_2} \\ \boldsymbol{\sigma}_{\boldsymbol{a}_1\boldsymbol{a}_2} & \boldsymbol{\sigma}_{\boldsymbol{a}_2}^2 \end{bmatrix}\right]$. The residuals were assumed to be normally distributed with a mean of 0, a residual variance of $\sigma_{e_i}^2$ for trait i, and a residual covariance between $\sigma_{\boldsymbol{e}_1\boldsymbol{e}_2}$: $\begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix} \sim \boldsymbol{N}\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \boldsymbol{I} \otimes \begin{bmatrix} \boldsymbol{\sigma}_{\boldsymbol{e}_1}^2 & \boldsymbol{\sigma}_{\boldsymbol{e}_1\boldsymbol{e}_2} \\ \boldsymbol{\sigma}_{\boldsymbol{e}_1\boldsymbol{e}_2} & \boldsymbol{\sigma}_{\boldsymbol{e}_2}^2 \end{bmatrix}\right]$.

The likelihood ratio test was used to determine whether genetic correlations among resilience indicators were significantly different from zero, by comparing modeled equation to a bivariate model with additive genetic covariance fixed at zero.

Results

Milk production and heat load

Table 1 presents the summary statistics of milk yield and heat load of the animals under study. No difference was detected in the heat load range for animals that calved during dry and wet seasons. However, the average milk yield of cows that calved during the dry season was higher than that of cows that calved during the wet season.

Response of milk yield to heat load at the population level

Similar responses in milk yield to increasing heat load were observed for the two seasons of calving and the full dataset, indicating an absence of seasonal contribution to the pattern of response of milk yield to heat fluctuations in our study. The analyses showed that, in the entire population, there was a decline in milk yield as the heat load increased. What differed over the population and across the two seasons was the rate at which milk production reduced with increasing heat load (Fig. 1). The milk production was lowest at THI 73.76, 74.68, and 71.43 for the combined population, animals calving in the dry season, and those that calved in wet season, respectively, before assuming a rising trend. Irrespective of the heat load, cows that calved during the dry season tended to produce more milk than those that calved during the wet season.

Fig. 2 illustrates the change in milk yield across the minimum–maximum normalized THI gradient of each environment at the population level. The environments under which the animals are reared had differential effects on the population response of milk yield to the increasing heat load. In the SAP environment, the milk yield decreased as the heat load increased throughout the experienced heat load range therein. In SH and SAA environments, the milk yield increased with an increase in heat load until THI 76.48 and 68.42, respectively, after which the milk yield declined with increasing heat load, possibly due to heat stress.

Additionally, a differential capacity for heat tolerance was evident for the animals depending on their genotype (Fig. 3). Animals in breed group (1) (≤ 50% *Bos taurus* genes) and breed group (3) (> 87.5% *Bos taurus* genes) acclimatized to heat load at THI 72.24 and 74.25, respectively. Animals with less than 50% *B. taurus* genes acclimatized to the heat load quickest and at the lowest THI. However, breed group (2) (50–87.5% *B. taurus* genetic makeup) showed a declining trend in milk yield to increasing heat load throughout the observed THI range.

Individual animal resilience phenotypes

Examples of individual animal reaction norms are illustrated in Fig. 4. These slopes reflect deviations from the population curves shown in Fig. 1 and constitute individual animal resilience phenotypes in two calving seasons, and when all animals were treated as one population. Considerable variation in milk yield responses to fluctuating heat load was demonstrated among individuals within

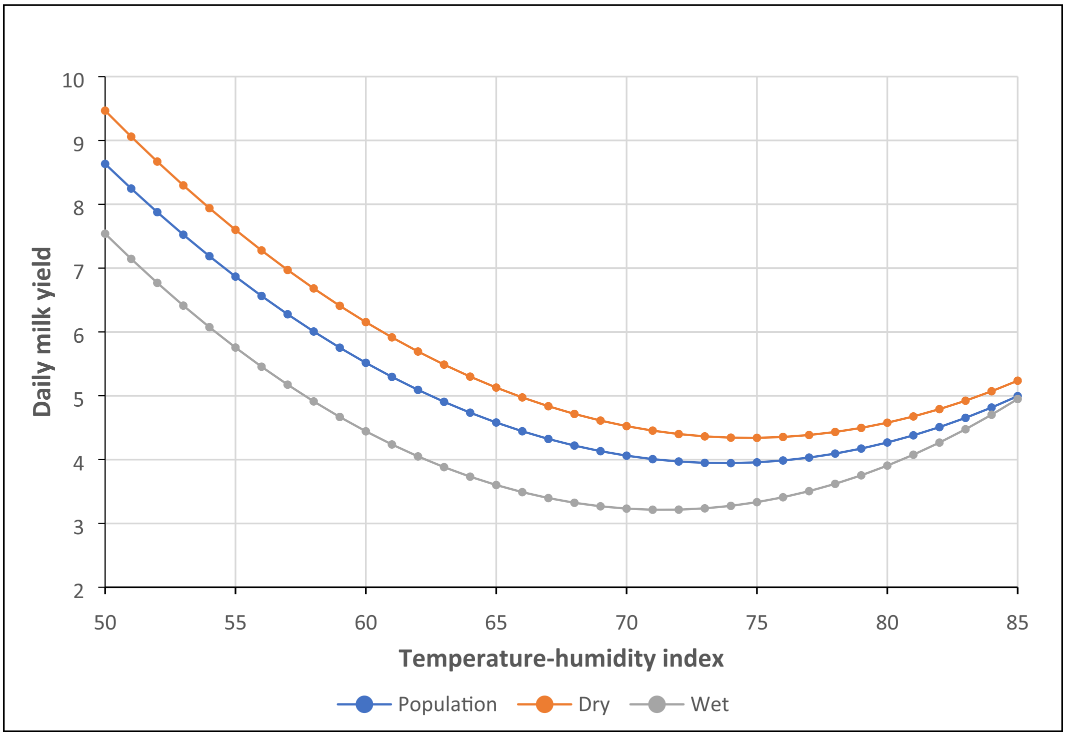

Fig. 1. Derived population reaction norms for the changes in 7-day average milk yield (daily milk yield, kg) in response to the average temperature-humidity index for all the cows (population), cows that calved during the dry season (dry) and cows that caved during the wet season (wet).

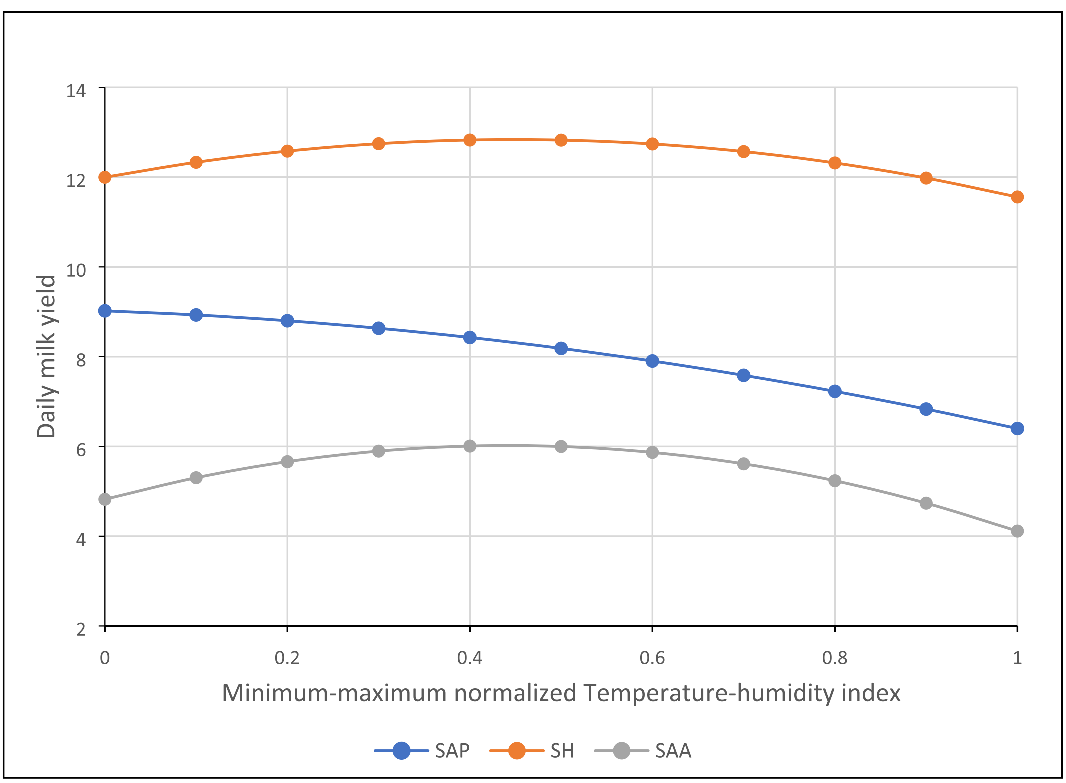

Fig. 2. Derived population reaction norms for changes in the 7-day average milk yield (daily milk yield, kg) in response to the minimum–maximum normalized average temperature-humidity index for cows kept under Semi-Arid Pasture (SAP), semi-humid (SH), and semi-arid arable (SAA) agroecological zones.

each group, especially at both ends of the THI range, signifying substantial GxE effects and a possibility of genetic improvement through selection.

Table 2 represents the descriptive statistics of the resilience phenotypes of individual cows. Slope1 and Slope2 denote changes in milk yield in response to heat load fluctuations at THI 50 and THI

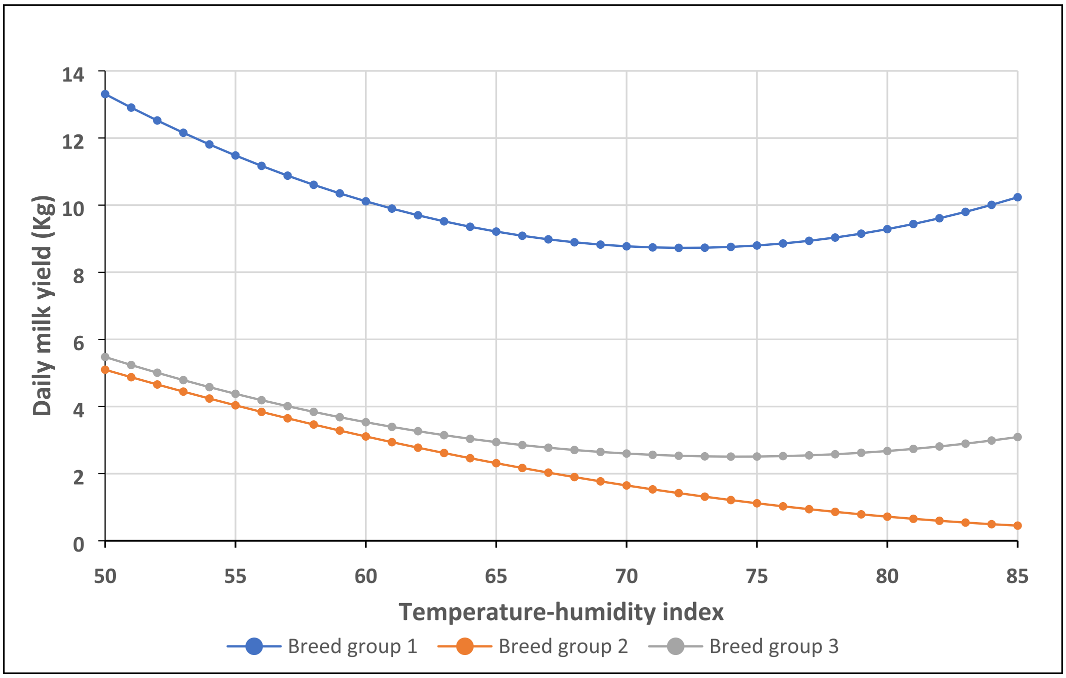

Fig. 3. Derived population reaction norms for changes in 7-day average milk yield (daily milk yield, kg) in response to the average temperature-humidity index for cows with ≤ 50% (Breed group (1), >50–87.5% (Breed group (2), and > 87.5–100% (Breed group (3) *Bos taurus* genes.

80, respectively. These two THI values were indicative of when the animals were not heat-stressed and when they were heat-stressed, respectively. Positive values of individual slopes indicate that milk yield increased with increasing heat load at the corresponding THI level and vice versa. A slope value close to zero implies that milk yield was generally unaffected by heat load changes. There was no substantial difference at descriptive level among similar resilience phenotypes based on the entire population and season of calving. The higher SD observed in all groups show higher variability in these resilience phenotypes, a phenomenon that is important for genetic analysis.

Factors affecting resilience phenotypes

Summary statistics from the least squares analyses of variance for different resilience phenotypes are presented in Table 3. No significant difference was observed among the three breed groups for the slope of the reaction norm at THI 50. Whereas there was no significant difference between BG1 and BG2 in slope2, BG3 had significantly lower Slope2 than BG1 and BG2. This implies that animals with > 87.5% *B. taurus* in their genetic makeup were significantly more influenced by heat stress at THI 80. Animals with less than 50% *B. taurus* genes in their genetic make-up had significantly the lowest absolute value of the slope of the reaction norm at both heat load levels ($P < 0.05$) indicating higher stability in response of milk yield to heat load. The environment also significantly affected all resilience indicators ($P < 0.05$) except slope2. Among the three environments, animals performing in the semi-arid pasture-based environment had the lowest slope1, showing the lowest response of cows' milk yield to heat load ($P < 0.05$). There was no significant difference in the cows' response of milk yield to heat load at THI 80 among the environments. Cows performing in the two semi-arid environments had significantly lower Absolute2 than those in the semi-humid environment showing a higher stability in milk production at THI 80 ($P < 0.05$).

Genetic parameters of resilience phenotypes

Variance components and genetic parameter estimates for resilience phenotypes are presented in Table 4. These parameters were estimated under no heat stress (THI 50) and heat stress conditions (THI 80) denoted by 1 and 2, respectively. Heritability estimates for almost all phenotypes at THI 50 (Slope1 and Absolute1) and THI 80 (Slope2 and Absolute2) differed significantly from zero ($P < 0.05$). This shows that a significant proportion of the observed phenotypic variation among animals was genetic. In all instances, slopes of the reaction norms had higher heritability estimate than absolute values of the reaction norm.

The correlation between resilience phenotypes and average milk yield is also shown in Table 4. All the phenotypes had significant ($P < 0.05$) and moderate-to-high genetic and phenotypic correlations with milk yield. Except Absolute1, all other phenotypes had significant phenotypic correlations with milk yield. Slope1 and Slope2 of both the entire population and the season of calving had positive and negative correlations with milk yield, respectively. This illustrates that the cows that responded more positively to heat load at THI 50 and those that responded more negatively to heat load at THI 80 had higher average milk yield. Both Absolute1 and Absolute2 had a positive genetic correlation with average daily milk yield, connoting that the cows with a stable milk production at THI 50 and THI 80 ultimately are on average unable to produce high total milk yield.

Phenotypic and genetic correlations among resilience indicators are presented in Table 5. A high positive correlation was observed between similar indicators derived for population and season of calving, indicating high genetic similarity between the indicators. In both instances, Slope1 and Slope2 had significant ($P < 0.05$) and moderate negative genetic and phenotypic correlations. This implies that the performance of cows that produce more milk at lower THI was greatly affected when they were exposed to higher THI and vice versa. Absolute1 and Absolute2 for both population and calving season datasets had significant positive genetic and

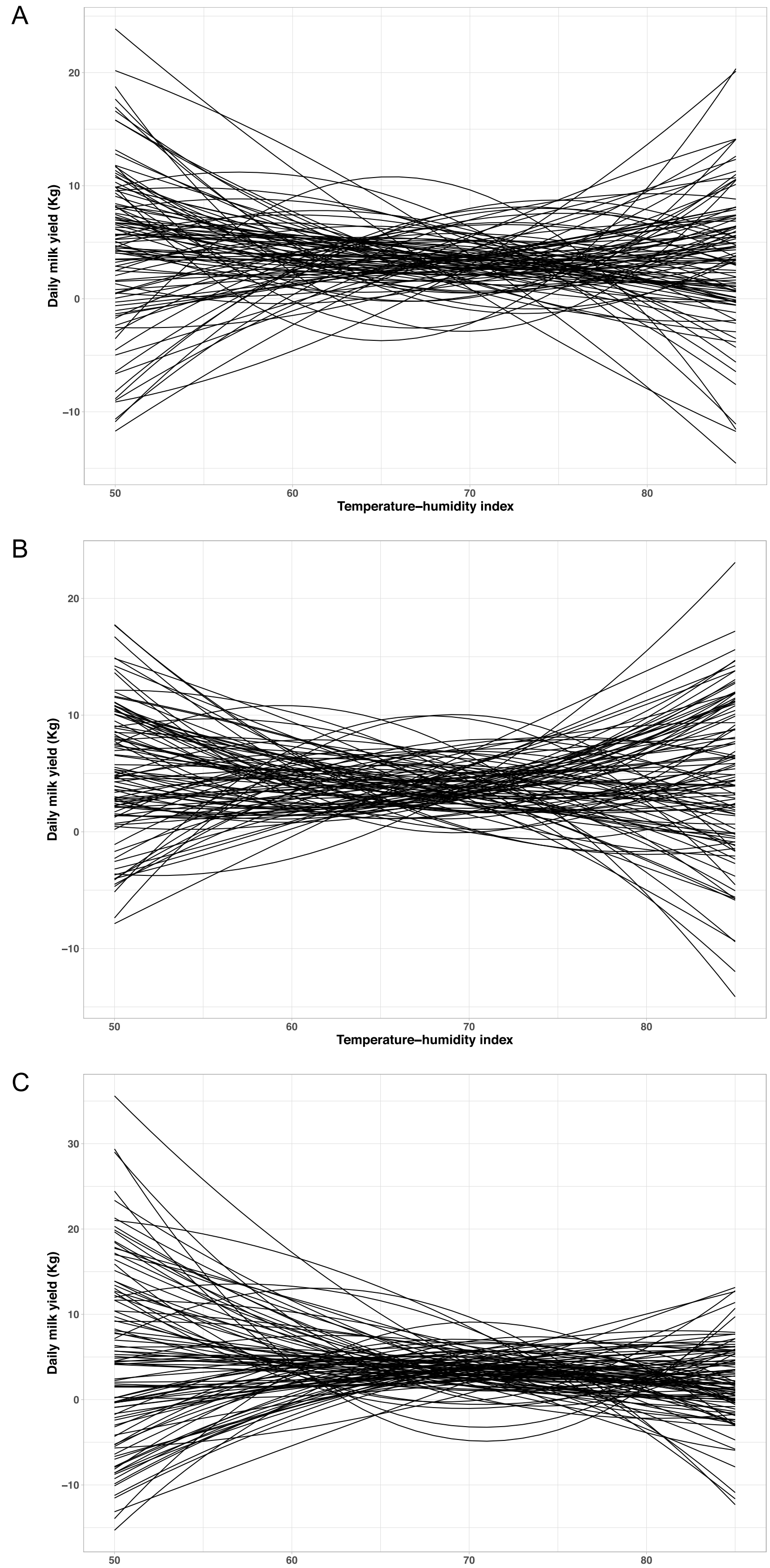

Fig. 4. Individual reaction norm showing changes in 7-day milk yield (daily milk yield, kg) in response to average temperature-humidity index (THI) for a random sample of 100 cows representing the entire population (A), wet season of calving (B), and dry season of calving (n = 100).

Table 2
Descriptive statistics (mean and SD in parentheses) of resilience phenotypes expressed as milk production change per unit increase in temperature-humidity index for the cattle population.

Data type	Slope1	Slope2	Absolute1	Absolute2
Population	−0.131 (0.756)	−0.025 (0.517)	0.701 (0.319)	0.567 (0.264)
Season-Specific	−0.110 (0.808)	−0.026 (0.437)	0.725 (0.327)	0.565 (0.264)

Abbreviations: Slope1 = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 50; Slope2 = performance change per unit change in temperature-humidity index at THI 80; Absolute1 = Absolute value of corresponding performance change (square root transformed) at THI 50; Absolute2 = Absolute value of corresponding performance change (square root transformed) at THI 80.

Table 3
Least square mean (LSM, SE in parentheses) by cattle breed and agroecological environment of resilience phenotypes expressed as milk production change per unit increase in temperature-humidity index.

Variable, and level	N	Population phenotypes				Seasonal phenotypes			
		Slope1	Slope2	Absolute1	Absolute2	Slope1	Slope2	Absolute1	Absolute2
Breed group (BG)									
BG1	689	−0.21(0.04)[a]	−0.002(0.03)[a]	0.68(0.02)[a]	0.54(0.01)[a]	−0.21(0.04)[a]	0.02(0.03)[a]	0.70(0.02)[a]	0.55(0.01)[a]
BG2	450	−0.24(0.04)[a]	−0.002(0.03)[a]	0.76(0.02)[b]	0.59(0.01)ab	−0.24(0.04)[a]	0.001(0.03)[a]	0.77(0.02)[b]	0.58(0.01)[ab]
BG3	600	−0.22(0.04)[a]	−0.07(0.03)b	0.74(0.02)[b]	0.60(0.01)[b]	−0.19(0.04)[a]	−0.08(0.03)[b]	0.76(0.02)[b]	0.61(0.01)[b]
Herd environment level									
SAP	499	−0.57(0.05)[a]	−0.04(0.04)[a]	0.73(0.02)[a]	0.55(0.02)a	−0.58(0.05)[a]	0.03(0.03)[a]	0.74(0.02)[ab]	0.55(0.02)[a]
SH	398	−0.01(0.04)[b]	−0.002(0.03)[a]	0.79(0.02)a	0.60(0.02)[b]	−0.02(0.05)[b]	0.004(0.03)[a]	0.79(0.02)[a]	0.60(0.02)[b]
SAA	842	−0.09(0.04)[b]	−0.03(0.03)[a]	0.67(0.02)[b]	0.54(0.01)[a]	−0.08(0.04)[b]	0.02(0.02)[a]	0.70(0.02)[b]	0.54(0.01)[a]

Abbreviations: Slope1 = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 50; Slope2 = performance change per unit change in temperature-humidity index at THI 80; Absolute1 = Absolute value of corresponding performance change (square root transformed) at THI 50; Absolute2 = Absolute value of corresponding performance change (square root transformed) at THI 80; SAP = Semi-arid pasture based agroecological zone; SH = Semi-humid agroecological zone; SAA = Semi-arid arable agroecological zone. Least square means sharing no superscript letter are significantly different at $P < 0.05$.

Table 4
Genetic parameters of resilience phenotypes (±SE) expressed as milk production change per unit increase in temperature-humidity index and correlation of the phenotypes with average daily milk yield for the cattle population.

Resilience Phenotype	V_A	V_E	V_P	h^2	r_g	r_p
Population						
Slope 1	0.093 ± 0.024	0.436 ± 0.026	0.529 ± 0.020	0.18 ± 0.044*	0.50 ± 0.090*	0.51 ± 0.019*
Slope 2	0.086 ± 0.015	0.174 ± 0.013	0.261 ± 0.010	0.33 ± 0.051*	−0.71 ± 0.053*	−0.48 ± 0.020*
Absolute 1	0.013 ± 0.005	0.084 ± 0.005	0.097 ± 0.003	0.13 ± 0.046*	0.618 ± 0.128*	0.08 ± 0.024
Absolute 2	0.012 ± 0.003	0.055 ± 0.003	0.067 ± 0.002	0.18 ± 0.049*	0.63 ± 0.121*	0.16 ± 0.024*
Calving season						
Slope 1	0.086 ± 0.024	0.513 ± 0.029	0.599 ± 0.021	0.14 ± 0.041*	0.40 ± 0.11*	0.41 ± 0.021*
Slope 2	0.085 ± 0.014	0.172 ± 0.013	0.256 ± 0.010	0.33 ± 0.051*	−0.64 ± 0.06*	−0.44 ± 0.021*
Absolute 1	0.007 ± 0.004	0.095 ± 0.005	0.102 ± 0.004	0.06 ± 0.04	0.74 ± 0.192*	0.08 ± 0.024
Absolute 2	0.008 ± 0.003	0.006 ± 0.003	0.066 ± 0.002	0.13 ± 0.044*	0.74 ± 0.140*	0.17 ± 0.024*

Abbreviations: Slope1 = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 50; Slope2 = performance change per unit change in temperature-humidity index at THI 80; Absolute1 = Absolute value of corresponding performance change (square root transformed) at THI 50; Absolute2 = Absolute value of corresponding performance change (square root transformed) at THI 80; V_P = Phenotypic variance; V_A = Additive variance; V_E = Residual variance; h^2 = heritability estimate; r_g = Genetic correlation; r_P = Phenotypic correlation. Asterisk denotes significance at $P < 0.05$.

phenotypic correlations indicating that stability in milk production of cows is maintained regardless of the THI level. Thus, a cow with a stable performance at THI 50 has a stable performance at THI 80. Whereas Slope2 and Absolute2 had a significant moderate negative genetic and phenotypic correlation, Slope1 and Absolute1 did not portray a substantial correlation for both population and calving season phenotypes.

Discussion

While the livestock industry is a known contributor to climate change, it is essential to recognize the reciprocal effects of climate change on livestock, particularly in tropical regions. Notably, the global rise in temperature, attributed to global warming, has heightened the heat stress experienced by livestock species and reduced overall livestock productivity. Selective breeding aimed at improving the animals' capacity to withstand increasing heat load, while maintaining optimal performance, could guarantee sustainable and profitable production of, and affordable access to animal-sourced food products. This study assessed phenotypes based on the response of milk production to changing heat load as potential indicators of heat tolerance in dairy cattle performing in SSA.

Despite a lack of difference in heat load range between cows that calved during dry and wet seasons, those that calved during dry season had significantly higher 7-day average milk yield. This observation could be attributed to the peak lactation milk yield, a determinant of lactation milk yield (Mellado et al., 2011). The environments under study have four seasons: two wet and two dry seasons with a dry season that lasts for 2–3 months and is followed by a wet season. Previous studies have shown that animals in this region reach their peak milk production between 2–3 months postcalving (Ojango et al., 2019; Ekine-Dzivenu et al., 2020; Oloo et al., 2022b). Therefore, it is most likely that cows that calved during the dry season peaked during the wet season when

Table 5
Genetic and phenotypic correlations (±SE) between different resilience phenotypes for the cattle population.

Resilience phenotype	r_g	r_P
Population Vs Season resilience phenotypes		
Population Slope1 Vs Season Slope1	0.98 ± 0.004*	0.98 ± 0.014*
Population Slope2 Vs Season Slope2	0.99 ± 0.007*	0.93 ± 0.003*
Population Absolute1 Vs Season Absolute1	0.97 ± 0.114*	0.80 ± 0.009*
Population Absolute2 Vs Season Absolute2	0.97 ± 0.031*	0.82 ± 0.008*
Similar phenotypes at different head load levels		
Population Slope 1 Vs Population Slope2	−0.58 ± 0.096*	−0.51 ± 0.019*
Population Absolute1 Vs Population Absolute2	0.60 ± 0.169*	0.21 ± 0.022*
Season Slope 1 Vs Season Slope2	−0.57 ± 0.104*	−0.52 ± 0.019*
Season Absolute1 Vs Season Absolute2	0.51 ± 0.156*	0.26 ± 0.023*
Different phenotypes at the same heat load level		
Population Slope1 Vs Population Absolute1	−0.14 ± 0.205	−0.16 ± 0.024*
Population Slope2 Vs Population Absolute2	−0.63 ± 0.133*	−0.14 ± 0.024
Season Slope1 Vs Season Absolute1	−0.44 ± 0.289	−0.12 ± 0.024*
Season Slope2 Vs Season Absolute2	−0.63 ± 0.155*	0.12 ± 0.024*

Abbreviations: Slope1 = performance change per unit change in temperature-humidity index at temperature-humidity index (THI) 50; Slope2 = performance change per unit change in temperature-humidity index at THI 80; Absolute1 = Absolute value of corresponding performance change (square root transformed) at THI 50; Absolute2 = Absolute value of corresponding performance change (square root transformed) at THI 80; r_g = Genetic correlation; r_P = Phenotypic correlation. Asterisk denotes significance at $P < 0.05$.

the feed supply was enough to support high milk production. Most animals that calved during the wet season (which normally lasts for 2–4 months) reached their peak lactation during the dry season when there were feed and water shortages which might have limited their milk production potential.

No substantial differences in the pattern of the response of milk yield to fluctuating heat load were observed in cows that calved during different seasons. This is probably because the differences in heat load between the dry and wet seasons in these environments are smaller and, in some cases, insignificant. Actually, it is mostly the amount of precipitation that is used to define seasons and not temperature or heat load.

At the population level, the milk yield of animals under study reduced with increasing heat load due to heat stress up to approximately THI 75 where the milk yield loss plateaued before it began to rise. This shows that the animals on average had acclimatized to the heat stress conditions beyond this THI (Ekine-Dzivenu et al., 2020). Exposure of animals to a prolonged high heat load makes them activate a process of acclamatory homeostasis (Horowitz, 2001). The process is characterized by a decline in the secretion of growth hormones, glucocorticoid, and catecholamine, leading to reduced metabolic heat production (Webster, 1991). The changes in hormonal profiles reduce feed intake, ultimately resulting in reduced milk production before acclimatization is reached. This explains the decline in milk yield at the population level before approximately THI 75.

Cows with less than or equal to 50% *Bos taurus* genes acclimatized to heat load at lower THI values and had the most stable milk production at higher THI values; hence, they were the most thermotolerant. This could be alluded to a higher percentage of *B. indicus* genes in their blood, which has been shown to enable the cows to be more thermotolerant and adapt well to prevailing harsh tropical production environments (Hansen, 2004; Renaudeau et al., 2012; Mwai et al., 2015; Kim et al., 2017). While the population reaction norm suggests that cows with more than 87.5% *B. taurus* acclimatized before those with > 50–87.5% *B. taurus*, further analysis revealed that this difference was not statistically significant. Cows with more than 87.5% *B. taurus* had significantly a lower slope of the reaction norm at THI 80 indicating a more pronounced negative impact of heat stress on this group. Moreover, no significant difference was observed between these two breed groups in all other resilience phenotypes.

A strong microenvironmental effect on the response of milk yield to heat load was evident. Cows performing in semi-arid environments showed a higher stability in performance at THI 80. Semi-arid environments are characterized by low rainfall and prolonged periods of drought (Jaetzold et al., 2006, 2010; Oloo et al., 2023a). The environmental stimulation and experiences in semi-arid environments helped the animals to acquire genetic/biological adaptation and evolved to survive in adverse heat load conditions (Parsons, 1994; Hansen, 2004; Gaughan et al., 2009).

A considerable portion of observed phenotypic variation in individual resilience phenotypes among cows stemmed from their genetic makeup. Heritability estimates of all resilience phenotypes were mostly significantly different from zero and ranged from 0.06 to 0.33. These estimates are within and slightly higher than the range previously reported (Sánchez-Molano et al., 2019; Tsartsianidou et al., 2021) for the same resilience phenotypes, but within the range reported for other resilience indicators and fitness traits (Berghof et al., 2019; Putz et al., 2019; Poppe et al., 2020, 2021b, 2021a; Oloo et al., 2023a). Similar to previous reports (Sánchez-Molano et al., 2019), we found that the slope of the reaction norm had higher heritability estimates than the absolute value of the slope of the reaction norm. These findings open up the potential for continuous improvement of heat tolerance in dairy cattle through targeted genetic selection.

The slope of the reaction norm at THI 50 and THI 80 had a moderate positive and negative genetic correlation with average milk yield, respectively. This implies that animals with high genetic merit for milk yield will produce high milk yield when not heat-stressed, but their milk production will be adversely affected under heat-stress conditions. On the other hand, although heat-tolerant cows generally produce low milk yield, their milk production profile is less negatively affected by heat stress (Gantner et al., 2015). These findings align with prior studies on heat stress, which demonstrated that cows possessing high genetic capacity for milk production tend to be more vulnerable to heat stress (West, 2003; Das et al., 2016; Sánchez-Molano et al., 2019). It is widely known that high-producing cattle typically exhibit lower THI thresholds compared to lower-producing cattle (Zimbelman et al., 2009; Cartwright et al., 2023). Milk production generates metabolic heat, and as production increases, the metabolic heat load also increases (Carabaño et al., 2017). So, for high-producing cows to maintain an optimal body thermal range during heat stress conditions, they tend to reduce their milk production. It is thus imperative to consider unfavourable correlations that may accompany any other trait of interest before incorporating these resilience phenotypes into the breeding goal. Developing and using the selection index approach would ensure an overall desirable genetic improvement by appropriately combining genetically antagonistic traits (van der Werf and Marshall, 2005; Dekkers and van der Werf, 2014; Mrode et al., 2021).

We noted a positive correlation between the absolute value of the slope of the reaction norm and average milk yield at THI 50 and 80. Animals with lower absolute values have a stable or less volatile response of milk yield to heat load. This observation confirms that cows with more stable milk production are generally low milk producers and vice versa.

High genetic similarity between indicators derived for population and seasons of calving further showed that the response of milk yield to heat load of individual animals based on season of calving and at population level followed a similar pattern. This infers that the variations in the season of calving in these environments did not invoke significant genetic differences in the response of milk yield to fluctuating heat load.

A negative correlation was observed between the slopes of the reaction norm at THI 50 and THI 80. Thus, cows that tended to have a higher response of milk yield at THI 50 had a lower response at THI 80, possibly due to reduced feed intake and metabolic inability to produce optimally at this thermal range. A positive genetic association between the absolute value of the slope of the reaction norm at THI 50 and THI 80 was evident. It signifies that a cow with stable milk production under heat-stress conditions is likely to maintain this stability when performing under optimal thermal conditions.

The observed negative correlation between Absolute 2 and Slope 2 denotes that under heat stress conditions, cows with a more stable performance tend to have a higher response of milk yield to heat load. The absolute value of the reaction norm looks at how close the response is to zero without considering the direction (+or -). Thus, the negative correlation between Absolute 2 and Slope 2 implies that these cows had generally a negative response of milk yield to heat load at THI 80 but heat-tolerant cows showed a less negative (or higher) response than their non-tolerant counterparts.

In general, this study has shown the possibility of utilizing reaction norms to measure the resilience of livestock species to varying weather conditions. Between the two indicators, the use of actual slopes, rather than their absolute values, provides a potentially more effective approach to quantifying resilience. This is because it allows for the selection of animals that exhibit enhanced performance in the direction of the anticipated climate change. This study has established that heat tolerance is negatively correlated with milk production potential. A multitrait selection index on resilience phenotypes might allow for the selection of heat-tolerant animals with improved milk production. High milk-producing cows exhibit a more pronounced increase in milk yield in response to rising heat load prior to experiencing heat stress. During heat stress conditions, only heat-tolerant cows have a stable performance. Therefore, a combination of a directional increase of animal performance up to the point where stress is triggered and stability of performance thereafter into an animal index would perhaps create the required balance between milk production and thermotolerance.

Conclusion

This study highlights the potential for selective breeding to enhance heat tolerance in dairy cattle in tropical countries. Heat stress negatively affects milk production, and dairy cows are able to acclimatize to heat stress conditions beyond a certain threshold. We used the slope of the reaction norm and its absolute value for changes in milk yield in response to heat load at different THI levels as distinct phenotypes of heat tolerance in dairy animals. These phenotypes are significantly heritable and hence can respond to genetic selection and be improved through targeted genetic interventions. However, such selection should consider the unfavorable correlations that exist between these and other traits of interest, such as milk yield, when incorporating them in selection indices and breeding goals. The study also found that higher milk-producing cows are more vulnerable to heat stress, while heat-tolerant cows tend to have stable milk production during such conditions. The use of actual slopes rather than absolute values as indicators of thermotolerance may offer a more effective approach to selecting animals with improved performance in the face of anticipated climate change. Ultimately, a multitrait selection index combining milk production potential with heat tolerance could strike a balance between milk productivity and thermotolerance. The research highlights the potential utility of reaction norms in measuring livestock resilience to varying weather conditions and provides valuable insights for enhancing heat tolerance in dairy animals in regions facing climate challenges such as sub-Saharan Africa through genetic selection.

Ethics approval

Not applicable.

Data and model availability statement

The data/models were not deposited in an official repository. Data are available upon request to the corresponding author.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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