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Research Article

Assessment of Phenotypic Plasticity in Dairy Production Traits of Toggenburg Goat Genotypes Across South African Agro-ecological Zones

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Abstract: The study evaluated phenotypic plasticity (PP) in reproductive and milk production traits of Toggenburg (TOG) goat genotypes across five South African agro-ecological zones (AEZ) using a longitudinal observational design. Data from 2,417 does representing five genotypes (Founders, CP, Appendix A, Appendix B, and StudBook Proper) were sourced from the Milch Breeders Society of South Africa LOGIX database. Descriptive statistics and least square means of reproductive, milk production, and dairy value traits were computed using GLM in Minitab 18.1. Four methods were applied to estimate the Phenotypic Plasticity Index (PPI): reaction norm-based, regression-based infinite-dimensional model, character trait, and variance-based approaches, with model performance assessed using p-values and R^2 values. The variance-based method revealed high PP for lactation milk yield ($s^2 = 394{,}324.2$ kg^2), somatic cell count ($s^2 = 929{,}621.7$ cells^2/mL^2), milk persistency ($s^2 = 3{,}511.05$), and lactation value index ($s^2 = 11{,}760.20$). Character trait analysis showed significant ($P < 0.05$) PP in somatic cell count, kid status score, litter size, and kidding ease score, particularly under humid and temperate conditions. Reaction norm models further confirmed significant PP in lactation milk yield, lactose, milk urea nitrogen, milk persistency, and lactation index, with R^2 values ranging from 27.11% to 99.64%. Regression-based infinite-dimensional models identified significant ($P < 0.05$) genotype-by-environment (GxE) interactions for dam longevity (1.0606 ± 0.2124), milk persistency (-2.481 ± 1.163), kidding ease score (-0.0423 ± 0.0209), and birth difficulty score (-0.0812 ± 0.0406). Conversely, age at first kidding and kidding interval exhibited non-significant PP ($P > 0.05$) across genotypes and AEZ, suggesting trait stability. Surface plots and phenotypic plasticity trends validated these findings. Overall, the study highlights substantial GxE interactions influencing Toggenburg goat adaptability, particularly with decreasing temperature and increasing humidity. Reaction norm and infinite-dimensional regression models were the most precise methods for quantifying PP. The findings underscore the value of integrating PP and GxE considerations into breeding programs to optimize productivity and resilience of Toggenburg goats under diverse environmental conditions.

Keywords: StudBook Proper, Dairy Value Traits, Decreasing Temperature, Increasing Humidity, Reaction Norm

Introduction

Through selective breeding programs, dairy goat stud breeding focuses on improving traits like conformation, health, and milk yield to provide superior breeding stock for enhanced herd productivity (Gipson, 2019; Bentley & Tranel, 2020). This is vital for commercial farms, as maintaining profitable milk yield and quality is key to their success (Van Suan & Hill, 2022).

Breeds like Toggenburg, Saanen, and Nubian are popular in the industry for their adaptability and excellent milk production (Van Suan & Hill, 2022). Toggenburg goats are known for their resilience and ability to produce milk under challenging conditions, making them highly adaptable to diverse environments (Mwato, 2025). Dairy goat production benefits both commercial and small-scale farms by generating revenue from fresh milk and value-added products such as cheese, yogurt, and goat milk soap (Miller & Lu, 2019). Goat milk is a staple in many low-income countries due to its accessibility and health advantages, such as easier digestion compared to cow milk, due to its smaller fat globules and unique protein composition (ALKaisy *et al.,* 2023; Da Silva and Da Costa, 2019). Additionally, the versatility of goat milk enhances its marketability and boosts producer profitability.

Genetic factors strongly influence goat milk production and reproductive efficiency (Taiwo-Idowu & Olufunke, 2017). In breeds like Toggenburg and other European goats, certain genes linked to milk yield and adaptation suggest that genetic selection can enhance traits such as heat tolerance and milk production (Getaneh & Alemayehu, 2022). These genetic factors are crucial for breeding programs aimed at optimizing goat performance in different environments. Environmental factors also play a significant role. Soil composition affects the nutritional quality of fodder, which influences goat nutrition and productivity (Furtak & Gałązka, 2019). Mineral content in the soil impacts the nutritional value of pasture, affecting both milk production and reproductive efficiency. Additionally, climate factors such as temperature and rainfall patterns influence feed availability, which in turn affects lactation periods and reproductive cycles (Godde *et al.,* 2021). Adaptations to these environmental variations are essential for maintaining consistent productivity across Agro-ecological zones. Management practices, including feeding strategies, breeding methods, and herd management, also significantly impact milk production and reproduction (Fodor *et al.,* 2018). While intensive systems may boost production, they require more resources, whereas extensive systems rely on natural adaptation to local conditions. Understanding the interactions between genetics, environment, and management is key to improving dairy goat production in diverse Agro-ecological zones (Mashamaite & Tada, 2025)

Understanding how Toggenburg goats adapt to different environments is essential, motivating the study of genotype-by-environment (GxE) interactions and phenotypic plasticity in these animals (Christensen *et al.,* 2021). GxE interactions, which reflect how genotypes respond differently to varying environmental conditions, significantly affect traits like growth, reproduction, and milk production (Sartori *et al.,* 2022). This emphasizes the need to consider both environmental and genetic factors when assessing livestock performance. Phenotypic plasticity, the ability of animals to produce different traits in response to environmental changes, is closely tied to GxE interactions (Sommer, 2020). In dairy goats, it helps identify genotypes that are more resilient and better suited to specific climates and management systems, which is crucial for improving sustainability and productivity in different Agro-ecological zones (Wang *et al.,* 2023; Zhang *et al.,* 2022; Vastolo *et al.,* 2024). Despite its importance, the phenotypic plasticity of Toggenburg goats has not been studied in South Africa, creating a knowledge gap that limits the development of locally tailored breeding programs. Reaction norm models are valuable tools for studying GxE interactions, providing accurate predictions of genotype performance across environments (Dekkers, 2021; Waters *et al.,* 2024). These models help breeders optimize productivity and adaptability to diverse conditions (Diouf *et al.,* 2020). By focusing on GxE interactions and phenotypic plasticity, this study aims to improve breeding strategies, enhance economic sustainability, and adapt Toggenburg goat farming to South African varied Agro-ecological zones. Therefore, the study evaluated the phenotypic plasticity of different Toggenburg goat genotypes in relation to milk production performance across Agro-ecological zones (AEZ).

Methodology and Analytical Procedures

Study Site, Animals, and Management

The study sites consisted of farms that were situated across the different AEZ across Limpopo, Gauteng, Eastern Cape, Free State, Northwest, Mpumalanga, Western Cape, Northern Cape and KwaZulu-Natal provinces. Table 1 shows the characteristics of AEZ in South Africa. The study used the data of stud TOG does (Figure 1) with dam parity ranging from 1-13. The animals were officially registered and participated in the Milk Recording and Performance Testing Scheme under the LOGIX database of South Africa.

Fig. 1: A mature dam of stud Toggenburg goat with kids

Animals were managed utilizing conventional husbandry and breed standards for feeding, vaccinating, health care, and breeding. The rearing of animals followed a semi-intensive production system. The flock spent the day foraging in the veld before making their way back to the pens at night. To meet the nutritional needs of the growing foetus and avoid pregnancy toxaemia, the feeding schedule for does in the final month of pregnancy was altered and supplemented with a concentrate mix. Water was given *ad libitum* throughout the goats' lifetime. A 1:20 mating ratio was used. Young bucks were taken out of the flock before they were ready to reproduce in accordance with the regulations of the breeding association. Prior to the start of the breeding season, chlamydia was treated for the prevention of abortion, along with internal parasites, nasal worms, and other conditions. Vaccinations against Bluetongue and Pulpy kidney were given annually.

Table 1: The Agro-ecological zones (AEZ) of South Africa and their bio-physical characteristics

Agro-ecological zone	Predominant province	Agro-ecological zones characteristics		
		Climate	Vegetation cover/Biomes	Landforms and soils
Arid	Northern Cape, parts of Limpopo, Northwest	Very low rainfall (<200 mm), High temperatures (20-30 °C)	Desert, Shrubland, Succulent Steppe	Sandy, low fertility (deserts, dunes)
Semi-arid	Northern Cape, Free State, Northwest, Eastern Cape (parts)	Low rainfall (200-400 mm), Moderate Temperatures (15-25 °C)	Grassland with scattered savanna trees, Thornveld	Sandy loam, moderate fertility (plains, plateaus)
Sub-humid	Limpopo (parts), Mpumalanga (parts), KwaZulu-Natal (parts), Eastern Cape (parts)	Moderate rainfall (400-600 mm), Moderate Temperatures (10-20 °C)	Savanna with woodland patches, Thicket, Grassland in valleys	Clay loam, moderate fertility (rolling hills, mountains)
Humid	KwaZulu-Natal, Limpopo (parts), Mpumalanga (parts)	High rainfall (800-1200 mm), Moderate Temperature (18-25 °C)	Shrubs, ferns, flowering plants	Clay loam, moderate fertility (low laying coastal plains and rolling hills)
Temperate	Western Cape (southwest), Eastern Cape (south)	Moderate rainfall (500-800 mm) with cool, wet winters mild temperatures (8-12 °C) and warm, dry summers warm temperatures (18-22 °C)	Fynbos with renosterveld (rhinoceros-field) patches, temperate forests	Sandy loam, moderate fertility (mountains, coastal slopes)

Source: FAO (2003)

Study Design, Data Collection, and Data Editing

The study utilized a longitudinal observational design to evaluate the phenotypic plasticity of TOG goat genotypes in different AEZ of South Africa. Genotypes used were classified according to blood purity as F0 (Founders), CP (<75%), B (75-87.5%), A (87.5-93.75%) and SP (>93.75%). Performance records from 17 farms (N = 2417 does) were extracted from the LOGIX database of the Milch Breeders Society of South Africa. The selected farms were purposively sampled to ensure representation across all five AEZs described under Table 1. Environmental variables such as average annual temperature, annual rainfall, humidity levels, and vegetation types were collected for each zone and are shown in Table 1. Animals with incomplete and inconsistent data related to birth and kidding dates, lactation performance and reproductive history were excluded to maintain data integrity. Additionally, breeders that did not adhere to standardized recording procedures or lacked sufficient historical data for longitudinal analysis were also excluded.

The sample size of does was determined by the availability of comprehensive performance records from the participating stud breeders. Although the distribution of dams differs across zones, the inclusion of breeders from all AEZs ensured a broad representation of environmental influence on TOG goat performance. The final conveniently determined sample size provided sufficient data for statistical analysis of phenotypic plasticity. Data gathered were classified into 3 categories, milk production, reproductive, and dairy value traits. Table 2 shows the description and measurement method of dairy goat production traits used in the study.

The data was captured in Microsoft Excel 2003. Birth season, birth year, dam longevity, age at first kidding (AFK), kidding interval (KI) and lactation length were determined from the date of birth, kidding dates, dam date of birth, and cancellation/death date. Other data and information gathered were litter size, breeder, sire ID, dam ID, and AEZ.

Data Analysis

To determine the significant fixed and random factors affecting dairy production traits was assessed using least-squares analysis of variance (ANOVA) through General Linear Model (GLM) function in Minitab 18.1 (2017) statistical software. The GLM, in matrix notation, is presented as $Y = Xb + Zu + e$, where Y = vector of observations (milk production, reproductive, and dairy value traits), b = vector of fixed effects (birth season, kidding season, birth year, genotype, AEZ, dam parity), u = vector of random effects (dam age, lactation length), e = vector of random residual effects assumed to be $N(0, \sigma^2)$. X and Z are incidence matrices relating responses to the fixed and random effects, respectively.

Table 2: Trait Description and method of measurements used in the study

Trait	Brief definition	Standard method of measurement and references
Milk production traits		
Lactation Milk Yield (LMY)	The quantity of milk a goat produces while lactating	Calibrated scale (Moran, 2015)
Fat (%) (FY)	Amount of fat a goat makes in its milk while lactating	Infrared spectroscopy (Daley *et al*., 2022)
Lactose (%) (LY)	A naturally occurring sugar found in milk	Infrared spectroscopy
Protein (%) (PY)	Amount of protein a goat makes in its milk while lactating	Kjeldahl method (Roy, 2020)
Somatic Cell Count (SCC)	A measure of number of somatic cells in a milk quality	California Mastitis Test (Sun *et al*., 2023; Rust *et al*., 2023)
Milk Urea Nitrogen (MUN)	An indicator of nitrogen efficiency, goat health, and environmental impact	Infrared spectroscopy
Reproductive traits		
Kidding Ease Score (KES)	Refers to the practice of assisting goats in giving birth with a minimum of stress and interruption	1 = Unassisted, 2 = mild assistance, 3 = requiring significant assistance, 4 = caesarean section
Kid Status Score (KSS)	Refers to the overall well-being and freedom from diseases of the individual animal during birth	1 = Strong and Vigorous Kids, 2 = Weak but Viable Kids, 3 = Weak and Non-Viable, 4 = Abnormal Kids (Constantin Cerbu *et al*., 2023)
Age at First Kidding (AFK)	The difference between the first kidding date and the birth date of the goat	Farm records (Rodriquez-Hernandez *et al*., 2022)
Kidding Interval (KI)	The interval between two consecutive kiddings in days	Farm records (Rodriquez-Hernandez *et al*., 2022)
Litter Size (LS)	The total number of kids a goat or doe has in one kidding	Direct count
Birth Difficulty Score (BDS)	Refers to dystocia scoring	1 = No Difficulty, 2 = Slight Difficulty, 3 = Moderate Difficulty, 4 = Severe Difficulty, 5 = Extreme Difficulty
Dairy value traits		
Lactation Index (LI)	A measure of a goat's milk production efficiency, calculated by combining various lactation traits	LI = total lactation milk yield (kg)/lactation length (days) (Da costa and Bluck, 2010)
Lactation Value Index (LVI)	A measure of a goat's lactation performance, considering both milk yield and persistency	LVI = (a x Milk Yield) + (b x Fat Yield) + (c x Protein Yield) + (d x Calving Interval). Where: *a, b, c*, and *d* are weighting factors that reflect the relative economic importance of each trait (Da costa and Bluck, 2010)
Milk Persistency (%) (MP)	Refers to a goat's ability to maintain milk production throughout the lactation period	MP = 100*(peak milk yield-post peak milk yield)/peak milk yield (Moran, 2015)
Dam Longevity (years) (DL)	Refers to the length of time a dam remains productive and able to breed, produce kids and milk until culling or death	Farm records (Hu *et al*., 2021)

The 3D surface plots were used to visualize the relationship between two independent and significant variables (genotype and AEZ) and one dependent variable at a time. The surface plot equation was represented as: $z = f(x, y) = \beta_0 + \beta_1 x + \beta_2 y + \beta_3 xy + \varepsilon$. Where z = Phenotype (dependent variable), x = Environment (independent variable), y = Genotype (independent variable), β_0 = Intercept, β_1 = Environmental sensitivity, β_2 = Genotypic effect, β_3 = GxE interaction coefficient, ε = Residual error assumed to be $N(0, \sigma^2)$. To determine Phenotypic Plasticity Index (PPI), four methods were used.

Linear Regression Model/Infinite-Dimensional Model

It is assumed that genotypes respond predictably and that environmental influences are constant. By considering environmental variation as an infinite-dimensional function, the infinite-dimensional model was expanded beyond linear regression. The phenotype *y* is modelled as a function of environmental conditions *E*. The linear regression model: $y_i = \beta_0 + \beta_1 E_i + \varepsilon_i$. where, y_i = observed phenotype for individual i. E_i = environmental factors (AEZs: arid, semi-arid, sub-humid, humid, temperate), β_0 = intercept, β_1 = slope (measuring the rate of trait change per unit environment), ε_i = residual error. The model was expanded into an infinite-dimensional model to allow non-linear, complex trait responses to environmental variation. $y_i = \int \beta(E)\, E_i\, dE + \varepsilon_i$. (Jamrozik & Schaeffer, 1997; Wilson *et al.,* 2005)

Reaction Norm Model

This model explains how the phenotype of a genotype varies in various environments (Gautier & Naves, 2011; Kelly *et al.,* 2012). A reaction norm model by Waters *et al.* (2024) in Minitab 18.1 (2017) statistical software was employed as follows: $P_i = \beta_0 + \beta_1 E_i + \beta_2 G_i + \beta_3 G_i x E_i + \varepsilon_i$. where P_i = dependent variable (reproductive, milk production, dairy value traits), β_0 = Intercept, β_1, β_2, and β_3 = are coefficients representing the linear effects of AEZ, genotype, and interaction effect, respectively. E_i = Environmental sensitivity representing the AEZ (arid = 1, semi-arid = 2, sub-humid = 3, humid = 4, temperate = 5). G_i = Genotypic effect (F0 = 1, CP = 2, B = 3, A = 4, and SP = 5), $G_i x E_i$ = Genotype-Environment interaction coefficient, ε_i = Residual error assumed to be $N(0, \sigma^2)$.

Character Trait Model/Coefficient of Variation (CV)

The Character Trait Model / Coefficient of Variation (CV) described by De Jong & Bijma (2002) and Murren *et al.* (2015) views the reaction norm as a collection of distinct and connected characteristics. Every phenotype was assumed to be unique to a given environment and was represented as a distinct trait. A multi-trait model was applied as: y = Xb + Zu + e where, Xb = fixed effects, Xu = random genetic effects, e = residuals assumed to be $N(0, \sigma)$. The CV was calculated as Standard deviation (SD)/mean traits ($\bar{x}$)*100.

Variance-Based Model

This model ascertains how environmental variations in trait variance occur. It aids in determining sensitivity to the environment (Rauw & Gomez-Raya, 2015; Sommer, 2020; Rovelli *et al.,* 2020). Total variance (V_P) was decomposed as follows: $V_P = V_G + V_E + V_{GxE}$ where: V_G = genetic variance, V_E = environmental variance, V_{GxE} = interaction variance.

Results

Descriptive Statistics of Study Variables

Table 3 provides descriptive statistics of study variable of stud Toggenburg goats in South Africa. The larger mean values represent desirable outcome for traits except BDS, KES, KS, SCC and MUN. A higher standard error shows more uncertainty whether the sample mean accurately represents the population mean. Higher standard deviation represents more variability among individual goats. A higher coefficient of variation value indicates more variation in that trait relative to the mean. Minimum and maximum values represent the range, showing the lowest and highest observations for each variable.

Factors Affecting Reproductive, Milk Production and Dairy Value Traits

The summary of fixed factors evaluated to influence traits in TOG is presented in Table 4. Significant factors were adjusted for during the determination of PPI. The 3D surface plots are presented to depict the response of traits to changing genotypes and AEZ. The response of TOG goats KES in different AEZ is shown in Figure 2. The findings demonstrated that KES is typically undesirable in the semi-arid (AEZ 2) and arid (AEZ 1) zones. The animals in Appendix A and F0 (AS Codes 1 and 2) category demonstrated higher KES, indicating undesirability. However, low KES were shown by the Appendix B and SP genotypes (AS Codes 3 and 4) particularly in the sub-humid (AEZ 3) and temperate (AEZ 4) zones, indicating that these genotypes are better suited to the zones. The surface plot on Figure 3 showed a comparatively flat surface with very minor differences in KSS among the various genotypes and AEZ suggesting a relatively constant performance from pure 50% to 100% blood purity and arid to temperate zones. Variations in AEZ and genotypes do not substantially affect the TOG goats' ability to produce healthy offspring with freedom from diseases during birth.

Table 3: Descriptive statistics of study variables for stud TOG goats

Variable	N	Mean	SE Mean	SD	CV (%)
Dam Age (months)	1657	74.644	0.868	35.347	17.35
Kidding Ease Score	2417	0.4617	0.0132	0.6506	14.91
Kid Status Score	2417	0.6045	0.0116	0.5682	23.99
Litter size	2417	1.7609	0.0132	0.6478	16.79
Birth Difficulty Score	2417	1.5784	0.0143	0.7022	14.49
Lactation Length (days)	2417	190.17	2.36	116.26	21.13
LMY (kgs)	2417	635.94	7.62	374.40	18.87
LFY (%)	2417	39.504	0.168	8.257	20.90
LPY (%)	2417	34.749	0.170	8.362	24.07
Dam weight (kg)	2417	54.786	0.242	11.882	21.69
SCC (x1000 cells/ml)	2417	386.73	4.52	222.18	27.45
Milk urea nitrogen (mg/dL)	2417	21.903	0.152	7.473	24.12
Lactation index	2417	90.043	0.650	31.951	15.48
Lactation value index	2417	229.05	2.92	143.66	12.72
Longevity (months)	754	86.55	1.90	52.13	20.23
Longevity (years)	754	7.114	0.156	4.285	20.23
Milk persistency (%)	2417	74.278	0.221	10.883	14.65

N: population size, SE mean: standard error of the mean, SD: standard deviation, CV: coefficient of variance, LMY: lactation milk yield, LFY: lactation fat yield, LPY: lactation protein yield, SCC avg: somatic cell count.

The same trend was observed with BDS across genotypes. Some variation in the number of kids per kidding among genotypes and AEZ as shown on Figure 4. A small degree of phenotypic plasticity in response to arid environmental conditions, is depicted. Although the overall variation is modest, different genotypes had impact on LS. Figure 5 shows a surface plot indicating differences in PY across genotypes and AEZs. Although there is a general tendency showing a rather steady PY, there have been minor variances noted based on the environment and genotype. On the other hand, the genotypes F0 (foundation stock) and SP (AS Code 4) showed marginally lower overall PY.

Table 4: Significant factors affecting milk production, reproductive and dairy value traits in Toggenburg goats

Trait	AEZ	TOG Genotype	Birth Season	Birth Year	Dam Parity	Breeder/Farm	Kidding Season
Milk production traits							
Milk Yield	NS	NS	NS	NS	**	NS	NS
Fat (%)	NS	NS	NS	NS	NS	**	NS
Lactose (%)	NS	-	-	***	NS	-	NS
Protein (%)	**	NS	NS	**	**	**	NS
Somatic Cell Count	NS	NS	NS	***	NS	*	**
Milk Urea Nitrogen	NS	NS	NS	NS	NS	***	NS
Reproductive traits							
Kidding Ease Score	**	NS	NS	***	NS	***	NS
Kid Status Score	***	**	NS	***	NS	***	**
Age at First Kidding	***	NS	***	***	-	-	-
Kidding Interval	NS	NS	NS	NS	-	-	-
Litter Size	***	NS	NS	***	***	***	NS
Birth Difficulty Score	NS	***	NS	***	NS	***	NS
Dairy value traits							
Lactation Index	NS	NS	NS	**	*	*	NS
Lactation Value Index	NS	NS	NS	*	NS	NS	NS
Milk Persistency (%)	NS	NS	NS	NS	**	NS	NS
Dam Longevity (years)	NS	NS	NS	***	NS	NS	NS

*NS = Not significant (P>0.10), * = significant at p<0.10, ** = significant at p<0.05, *** = significant at p<0.001, - = value missing, no records observed.*

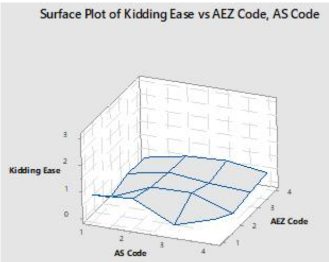

Fig. 2: Kidding ease score response

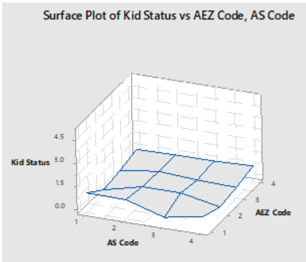

Fig. 3: Kid status score response

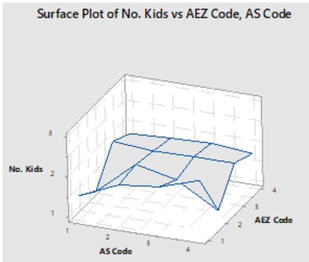

Fig. 4: Litter size response

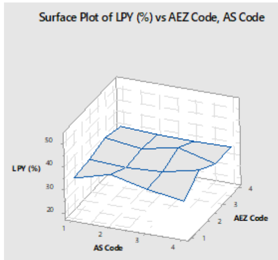

Fig. 5: Protein yield response

Assessment of Phenotypic Plasticity Index (PPI) Using Different Methods

Variance-based and Coefficient of Variance Method (CV)

Table 5 presents the variation and coefficient of variation (CV) for the traits. Notable plasticity signified through a high variance across genotypes and environments, were observed on LMY, SCC, KI, LI, LVI, and MP. Traits such as FY, PY, KES, KSS, LS and BDS indicated less variation across genotypes and AEZ, thus there was no phenotypic plasticity.

The CV method indicated significant plasticity on reproductive traits such as KES, KSS and LS in humid and temperate regions suggesting a substantial sensitivity to genotypic variations. Similarly, LS exhibited a higher CV in the arid, semi-humid and temperate zones. Conversely, LMY, FY, LY, PY, MUN, KI, AFK, BDS, LI, LVI, MP, and DL showed no significant plasticity (*P>0.05*), exposing relative stability among genotypes across AEZ.

Reaction Norm-based Method

Table 6 presents reaction norm analysis results. This analysis revealed significant phenotypic plasticity in several traits of Toggenburg goats, particularly concerning reproductive performance and dairy value. Notably, KES (R^2 = 65.04%), BDS (R^2 = 27.11%), KSS (R^2 = 63.81%), LY (R^2 = 81.58%), LMY (R^2 = 99.64%) and MUN (R^2 = 48.59%) exhibited significant (*P<0.05*) phenotypic plasticity, indicating strong environmental influences. Additionally, LI, LVI, and MP also demonstrated significant (*P<0.05*) phenotypic plasticity. In contrast, FY, PY, SCC, AFK, KI, and LS all indicated no significant (*P>0.05*) phenotypic plasticity. This implies that the relationship between genotype and phenotype is not significantly altered by environmental variation across AEZ.

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Table 5: Phenotypic plasticity index values of Toggenburg traits derived through variance-based and coefficient of variation method

Trait	Variance-Based Method	Coefficient of Variation (CV) Method by Environment					p-value	R^2
		Arid	Semi-Arid	Semi-Humid	Humid	Temperate		
Milk production traits								
Fat (%)	0.5484	10.05	20.33	8.16	16.25	19.94	0.128	79.12
Milk Yield	394324.2	34.91	57.58	48.84	57.46	69.66	0.770	99.64
Lactose (%)	1.6586	6.73	7.06	4.34	*	12.36	0.508	81.58
Protein (%)	0.8847	8.43	10.22	8.54	745.23	15.34	0.062	81.31
Somatic Cell Count	929621.7	102.34	70.15	82.12	*	94.91	0.032	35.78
Milk Urea Nitrogen	29.998	12.52	12.61	22.90	*	19.25	0.112	48.59
Reproductive traits								
Kidding Ease Score	0.3175	0.00	0.00	0.00	12.34	35.21	0.010	65.04
Kidding Interval	1722.85	10.37	12.19	11.88	*	12.01	*	*
Age at First Kidding	1.738	10.80	10.04	7.98	*	10.23	*	*
Kid Status Score	0.1881	0.00	0.00	0.00	12.34	19.67	0.000	63.81
Litter Size	0.5406	42.34	34.39	40.15	19.37	41.80	0.001	19.88
Birth Difficulty Score	0.4926	44.76	38.79	26.82	33.08	35.93	0.073	27.11
Dairy value traits								
Lactation Index	1020.575	27.21	53.82	27.23	*	29.19	0.710	61.09
Lactation Value Index	11760.20	65.47	64.13	76.95	65.35	78.21	0.835	46.41
Milk Persistency (%)	3511.05	68.94	68.58	72.98	*	77.13	0.058	67.17
Dam Longevity (years)	6.5201	69.57	39.92	40.80	*	42.70	0.193	82.57

* = *Value missing, no records observed*

Table 6: Phenotypic plasticity index values of Toggenburg traits derived through reaction norm-based method

Trait	Reaction Norm-based Method by Genotypes					p-value	R^2
	F0	CP	B	A	SP		
Milk production traits							
Fat (%)	-0.0244	-0.0307	-0.0396	-0.0308	-0.0345	0.419	79.12
Milk Yield	0.1023	0.0042	0.1452	-0.0067	0.0147	0.010	99.64
Lactose (%)	0.0080	0.0027	-0.0123	0.0077	-0.0204	0.000	81.58
Protein (%)	-0.0088	-0.0232	-0.0201	-0.0135	-0.0117	0.062	81.31
Somatic Cell Count	-0.0335	-0.1117	0.0027	0.1742	0.0806	0.929	35.78
Milk Urea Nitrogen	0.0421	-0.0228	0.0089	0.0366	0.0264	0.011	48.59
Reproductive traits							
Kidding Ease Score	-0.0612	-0.0154	-0.0187	-0.0434	-0.0632	0.000	65.04
Age at First Kidding	0.0377	-0.0047	-0.0171	0.0058	0.0022	0.708	0.05358
Kidding Interval	-0.0248	-0.0088	-0.0133	0.0019	-0.0015	0.811	0.02215
Kid Status Score	-0.0186	-0.0582	-0.0199	-0.0164	-0.0187	0.000	63.81
Litter Size	0.0075	-0.0892	-0.0361	-0.0231	-0.1203	0.439	19.88
Birth Difficulty Score	0.3695	0.0741	0.0201	-0.0201	-0.0630	0.014	27.11
Dairy value traits							
Lactation Index	0.0632	-0.0654	0.0938	-0.0218	0.0813	0.006	61.09
Lactation Value Index	0.0840	-0.0422	-0.0794	-0.0525	-0.0577	0.019	46.41
Milk Persistency (%)	-0.0235	0.1200	-0.0094	0.0013	0.0032	0.013	67.17
Dam Longevity (years)	-0.0551	0.0299	0.1070	0.0702	0.0222	0.067	82.57

Regression-based Infinite-dimensional Model Method

Table 7 presents the results of infinite-dimensional model analysis. SCC, MP, and DL exhibited significant (*P<0.05*) phenotypic plasticity, with the effect of genotype varying substantially across different AEZs. This suggests that environmental factors within different AEZs influence the expression of genetic potential for SCC. BDS also showed a statistically significant (*P<0.05*), albeit weaker, interaction between genotype and AEZ, implying some degree of environmental influence on the genetic predisposition to birth difficulties. For traits such as LMY, FY, LY, PY, MUN, KES, KSS, AFK, KI, LI, and LVI, the lack of a significant interaction (*P>0.05*) suggests that the effects of genotype on these traits are relatively consistent across the different AEZ studies.

Table 7: Phenotypic plasticity index values of Toggenburg traits derived through regression-based infinite-dimensional model method

Trait	Regression-Based Method				p-value	R^2
	Intercept	β_1 - Genotype	β_2 - AEZ	Interaction		
Milk production traits						
Milk Yield	983.6±166.5	-3.925±59.86	32.33±36.15	-7.711±12.47	0.5365	79.12
Fat (%)	4.487±0.1651	0.0033±0.0593	-0.1058±0.0358	-0.0021±0.0124	0.8631	99.64
Lactose (%)	4.193±0.0706	0.0469±0.0254	0.04249±0.0153	-0.0128±0.0053	0.0154	81.58
Protein (%)	3.492±0.8373	-0.0645±0.0301	-0.0634±0.0182	0.0054±0.0063	0.3886	81.31
Somatic Cell Count	1910±251.4	-313.2±90.47	-156.1±56.60	55.97±19.19	0.0036	35.78
Milk Urea Nitrogen	28.27±1.422	-0.3262±0.5088	-0.0505±0.3379	0.1479±0.1104	0.1808	48.59
Reproductive traits						
Kidding Ease Score	1.893±0.4073	0.0423±0.1024	0.1072±0.0834	-0.0423±0.0209	0.0437	65.04
Kid Status Score	2.123±0.2755	-0.0212±0.0693	-0.1227±0.0563	0.0212±0.0141	0.1342	*
Age at First Kidding	13.19±0.5595	-0.0456±0.1552	-0.1253±0.1661	0.0247±0.0465	0.5948	*
Kidding Interval	370.4±19.25	-4.733±5.408	-4.504±5.694	1.141±1.617	0.4807	63.81
Litter Size	1.476±0.5306	0.1176±0.1334	0.0769±0.1084	-0.0286±0.0272	0.2932	19.88
Birth Difficulty Score	0.4263±0.8935	0.4146±0.2009	0.2959±0.1803	-0.0812±0.0406	0.0455	27.11
Dairy value traits						
Lactation Index	80.59±7.927	3.509±2.837	3.012±1.759	-0.5084±0.5984	0.3958	61.09
Lactation Value Index	176.5±28.34	0.7631±10.19	0.7632±6.151	-1.946±2.122	0.3593	46.41
Milk Persistency (%)	16.52±15.35	13.99±5.514	11.06±3.408	-2.481±1.163	0.0332	67.17
Dam Longevity (years)	2.485±1.283	-0.09272±0.8631	0.7894±0.2584	*	0.0024	82.57

** = Value missing, no records observed*

Discussion

Assessment of Phenotypic Plasticity Index Using Different Methods

Analysis of variance and coefficient of variation (CV) revealed significant phenotypic plasticity in SCC, KSS, LS, and KES, indicating that environmental factors significantly influence these traits. The temperate zone exhibited the highest CV for SCC, suggesting heightened environmental sensitivity, a finding consistent with research on German Holstein dairy cattle (Nada *et al.,* 2024). Similarly, the greatest plasticity in KSS was observed in the temperate zone, whereas the arid, semi-arid, and semi-humid zones showed no variation. This pattern of environmental dependence contrasts with the findings of Grazer & Martin (2012), who reported that reproductive traits such as kid viability were highly influenced by climatic factors, highlighting that an increase in humidity decreases the temperature. LS displayed greater variation in the semi-humid and temperate zones, which supports studies in Murciano-Granadina goats indicating that litter size is highly responsive to environmental conditions where there is an increase in humidity (Mokhtari *et al.,* 2024). KES, which also exhibited significant plasticity, followed a similar trend, with no variation in the arid, semi-arid, and semi-humid zones but increased sensitivity in the humid and temperate regions. This also emphasizes the inversely proportionality relationship between humidity and temperature. These results agree with observations in cattle, where calving ease was more influenced by climate and nutrition in temperate zones compared to arid regions (Muzzo *et al.,* 2024).

In contrast, FY, LMY, LY, PY, MUN, KI, AFK, BDS, LI, LVI, MP,and DL exhibited no significant phenotypic plasticity ($P > 0.05$), suggesting that these traits are relatively stable across different AEZ. However, intra-zonal variations were observed, with MP showing the highest CV in the temperate zone where there is high humidity, and low temperature, DL exhibiting greater variation in the arid zone where there is high temperature and low humidity. The stability of milk composition traits is consistent with findings in Saanen, Alpine, and Nubian goats (Shuvarikov *et al.,* 2021), where protein and fat content showed minimal environmental influence. Likewise, Gross (2022) reported that breeds intensively selected for milk production, such as Holsteins, tend to produce more milk than dual-purpose or beef breeds; however, long-term selection of strains within a breed under different environmental conditions may lead to divergent lactational performance. The limited plasticity observed in reproductive traits such as KI and AFK aligns with studies on crossbred dairy goats, indicating that these traits are strongly genetically controlled with limited environmental responsiveness (Desire *et al.,* 2017).

Reaction norm analysis revealed significant phenotypic plasticity in several traits of TOG goats, particularly in reproductive performance and dairy value. Notably, LY, KES, and KSS exhibited strong environmental influences, indicating a high degree of GxE interaction. Similar results have been reported in

Saanen goats, where lactose content and reproductive traits demonstrated significant variation across climatic zones (Kljajevic *et al.,* 2018). Furthermore, LI, LVI, and MP displayed significant plasticity, suggesting that these traits are responsive to genotypic variation, a trend also observed in Murciano-Granadina goats (Mokhtari *et al.,* 2024). LMY and MUN in F0 genotype showed significant plasticity, which reinforces previous findings that milk production and composition traits in dairy goats are strongly affected by environmental conditions, highlighting the increase in purity levels of TOG goats (Kljajevic *et al.,* 2018; Zhu *et al.,* 2020). The high R^2 value for LMY suggests that genetic expression for this trait is highly influenced by Agro-ecological conditions, which aligns with findings in Damascus goats, where milk yield responded significantly to climate and feeding variations (Yakan *et al.,* 2019). BDS also exhibited significant plasticity, implying that environmental stressors play a role in KES, a trend similarly noted in Alpine goats (Sejian *et al.,* 2021). Conversely, FY, PY, SCC, AFK, KI, and LS did not exhibit significant phenotypic plasticity ($P > 0.05$), indicating that these traits remain relatively stable across different genotypes. These results align with previous studies on dairy breeds, where milk fat and protein contents were found to be largely genetically determined with minimal environmental impact (Galli and Risé, 2017). Similarly, litter size and kidding interval have been reported as traits with strong genetic control, showing low responsiveness to environmental variation in dairy goat breeds (Chen *et al.,* 2025).

The regression-based model analysis revealed significant phenotypic plasticity in several traits of TOG goats, highlighting the influence of environmental variation on genetic expression. SCC exhibited strong plasticity, suggesting that the genetic potential for SCC is highly dependent on AEZ. This finding is consistent with previous studies on dairy cattle and goats (Dahl & McFadden, 2022; Desidera *et al.,* 2025), where SCC was found to vary significantly across different environmental conditions, likely due to heat stress and pathogen exposure. Similarly, DL displayed a significant GxE interaction, indicating that lifespan in dairy goats is influenced by environmental stressors, a trend also reported by Sejian *et al.* (2021). MP showed significant plasticity, reinforcing its sensitivity to environmental variation. This supports previous findings (ALKaisy *et al.,* 2023), where persistence was found to be influenced by management practices, nutrition, and climate other than genetics influences. BDS also exhibited significant plasticity, implying that environmental conditions contribute to variation in kidding ease. Similar results have been observed in Damascus goats, where heat stress and nutritional deficiencies were linked to increased birth difficulties (Kerr, 2010).

In contrast, traits such as LMY, FY, LY, PY, MUN, KES, KSS, AFK, KI, LS, LI, and LVI did not show significant GxE interactions. This suggests that the genetic influence on these traits remains relatively stable across AEZ, corroborating previous studies on dairy cattle (Mancin *et al.,* 2024). Notably, the lack of significant plasticity for milk composition traits contrasts with findings in Saanen and Murciano-Granadina goats, where fat and protein percentages were found to be largely under genetic control with minimal environmental impact (Kljajevic *et al.,* 2018).

The 3D Surface Plots Response of Toggenburg Genotype to Variation Across Agro-ecological Zone

The findings indicate that KES in TOG goats is significantly influenced by GxE interactions. Specifically, the semi-arid and arid zones (AEZ 2 and AEZ 1, respectively) were associated with more difficult kidding, particularly in F0 and Appendix A genotypes (AS Codes 1 and 2). This aligns with previous research by Robertson *et al.* (2020), which highlights those harsh environmental conditions, such as heat stress, low-quality fodder, and water scarcity, can impair animal health and increase the risk of dystocia. The observed challenges in KES under harsh environments where temperature is high could stem from impaired muscle function and reduced energy reserves in does, making labor more difficult. These findings emphasize the importance of considering environmental stressors in breeding programs aimed at improving kidding ease.

In contrast, Appendix B and StudBook Proper genotypes (AS Codes 3 and 4) exhibited better KES, especially in the sub-humid and temperate zones (AEZ 3 and AEZ 4), showing the improvement of the TOG blood purity levels in more humid regions. This suggests that these genotypes are better suited to the environments where there is high humidity, low temperature, adequate rainfall, and favorable grazing conditions promote better reproductive outcomes (Underwood *et al.,* 2015). This GxE interaction underscores the need to select and breed goats that are well-adapted to specific environments. Hiranya *et al.* (2015) stated that incidences of dystocia in small ruminants are more common under stressful environments. These results highlight the importance of genetic adaptation and environmental factors in determining KES, and they corroborate the findings of the present study.

The 3D surface plot for KSS revealed a relatively flat surface, indicating limited phenotypic plasticity and a consistent kid status across genotypes and AEZs. This suggests that TOG goats possess a degree of resilience in their ability to produce healthy offspring, even under varying environmental conditions. This finding is supported by Ramachandran & Sejian (2022), who noted the resilience of dairy goats in their reproductive performance, particularly when raised in regions with fluctuating climate conditions. Nair *et al.* (2021) similarly demonstrated that goats' natural resistance to external stressors was unaffected by environmental challenges like heat stress and limited feed. The biological basis for this resilience may lie in the goats' physiological adaptations that allow them to maintain relatively stable reproductive functions despite environmental variations.

The surface plot for litter size showed some variation among genotypes and AEZs, with a slight decline in the number of offspring in semi-arid and arid zones, particularly for genotype AS Code 4 (SP). This suggests that while TOG goats exhibit some consistency in LS across most AEZs, there is a degree of phenotypic plasticity in response to environments with high temperature and low humidity. These results are consistent with Adjassin *et al.* (2022) and Mataveia *et al.* (2021), who reported that harsh weather conditions can negatively impact prolificacy. The observed reduction in LS in arid conditions could be attributed to decreased reproductive efficiency under environmental stress due to high temperatures, potentially affecting ovulation rates and embryo survival (Sánchez-Dávila *et al.,* 2015).

The study revealed that better pasture quality and nutritional availability in temperate and sub-humid areas led to increased PY in TOG goats. This is in line with Zhu *et al.* (2020), who found similar results. Conversely, environmental stresses in arid and semi-arid zones often result in decreased milk protein output, likely due to the relationship between heat stress and forage quality because of high temperature and low humidity in the regions (Jaber *et al.*, 2019; Ramón *et al.*, 2021). However, the genotypic adaptation can help maintain protein yield stability in increasingly difficult environments (Mullualem *et al.*, 2024).

Conclusions

The study highlights the importance of considering GxE interactions in breeding programs for TOG goats. Among the methods assessed for evaluating phenotypic plasticity in dairy goats, the reaction norm-based method and regression-based method proved to give more details demonstrating significant interactions between genotype and environment. While some traits, such as KSS and LMY, exhibit relatively low phenotypic plasticity, others, such as KES and PY, are significantly influenced by environmental conditions. A change in environmental condition i.e., decrease in temperature and increase in humidity (arid to temperate) indicated significant phenotypic plasticity of TOG genotypes on milk production, reproductive and dairy value traits. The findings emphasize the need for targeted breeding strategies that account for the specific challenges and opportunities presented by different AEZs.

Farmers and breeders should develop separate breeding objectives for different AEZs, focusing on selecting goats that are well-adapted to the specific environmental conditions of each zone. In arid zones, heat stress tolerance, water use efficiency, and the ability to thrive on low-quality forage are the prized traits. A match of genotypes to environments based on performance characteristics is envisaged. Appendix B and StudBook Proper genotypes appear to be better suited to more favorable humid and temperate environments, while F0 and Appendix A genotypes may be more appropriate for arid and semi-arid environments. The implementation of management practices that mitigate the negative effects of environmental stressors is paramount, such as providing supplemental feeding during periods of drought, ensuring access to clean water, and providing shade to reduce heat stress. Future research should identify specific genes and physiological mechanisms that contribute to environmental adaptation in Toggenburg goats.

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Data will be made available on request by the corresponding author.

Author Contributions

Obert Tada: Conceptualization, Study Design, Methodology and Statistical Analysis, Supervision and Guidance.

Tshepho Matshebuka: Data Acquisition, Manuscript Preparation and Original Draft, Manuscript Review and Editing, Final Approval.

Louis Thobela Tyasi: Methodology and Statistical Analysis, Supervision and Guidance, Manuscript Review and Editing, Final Approval.

Conflict of Interest

The authors declare no competing interest.

Ethics Statement

Ethical approval for this study was obtained from the University of Limpopo Animal Research and Ethics Committee (ULAREC) (AREC-290914-017).

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