HETEROGENEITY OF VARIANCE FOR MILK PRODUCTION TRAITS BETWEEN THE LOW AND HIGH INPUT DAIRY PRODUCTION SYSTEMS OF SOUTH AFRICA

By

MARCUS NKETE TLABELA

MINI-DISSERTATION

SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

MASTER OF SCIENCE
IN
AGRICULTURE (ANIMAL PRODUCTION)

IN THE

DEPARTMENT OF AGRICULTURAL ECONOMICS AND ANIMAL PRODUCTION,
SCHOOL OF AGRICULTURAL AND ENVIRONMENTAL SCIENCES

AT THE

UNIVERSITY OF LIMPOPO

SUPERVISOR: PROF. CB BANGA

CO-SUPERVISOR: DR. B DUBE

: DR. O TADA

2020

DECLARATION

“I declare that HETEROGENEITY OF VARIANCE FOR MILK PRODUCTION TRAITS BETWEEN THE LOW AND HIGH INPUT DAIRY PRODUCTION SYSTEMS OF SOUTH AFRICA, is my own work and has not previously been submitted to any tertiary institution of higher education and training. I further declare that all sources cited or quoted are indicated and acknowledged by means of a comprehensive list of references”.

……………………………………	…..………………………
MARCUS NKETE TLABELA	DATE

DEDICATIONS

This dissertation is dedicated to my late mother Andricca Tlabela, who always emphasised the importance of education and business. My family and friends, thanks for keeping the cash flowing through out the study. This is dedicated to the future, motivated by the past.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude and appreciation to Prof Banga, Dr Dube and Dr Tada for accepting me as their student and mentorship. I would also like to extent my many thanks to Ms TF Kekana, Ms NN Makhubele, Ms MJ Selapa Mr ME Maake,Ms Mothotse Sello and my team,you guys made it look easy no matter the situation. My big sister, Ingrid Phuti Tlabela, you have been a pillar of strength and of course Rankotsana Ramokolo and Mokgopo Masekwameng how can I leave you guys, thank you from the bottom of my heart.

Rapau Samson, Mako Evidence, Maja Tshepho, Tlou Tlabela, Njabulo Sithole, Ramakgopa Moditja, Molekwa Mmasabatha, Mahlwele Lesedi, Kudumela Refiloe, Montjane Mohlompegi,Legodi Sekgogokgobo, Phahlamohlaka Matsebe,Khumalo Ntomizodwa, Makwela Kamogelo, Kekana Khutso, Nkadimeng Lekoko, Mathekga Justice(Adv.),Tema Alfred, Mampone Kwena, Sebjeng Phaphedi, Mabuzela Gomolemo, Boloka Pheeha, Mamidza Naho, Silence Shipalana and everyone whom we shared good and bad memories in this journey, this is your success too. I appreciate your presence and support. Ga modimo ale dire ka go loka, tsa lena di le lokele. Ivory park taxi association, chairman of Tembisa Pretoria taxi association sub-rank, Ntate Sibiya (M'dala) thank you for always waiting and making sure we get to school (research).

This study would have not been successful without the financial assistance from National Research Foundation NRF-VLIR and University of Limpopo. I want to express my gratitude to Prof, K Ayisi for giving me an opportunity and having faith in me. The Executive Dean's office and the VC and Principal, Prof. Mahlo Mokgalong for support throughout this study Thank you to the Integrated Registration and Genetic Information System (INTERGIS) for providing the data which without it this study wouldn't have been possible. Thank you to all several researchers, staff and students at the Agricultural Research Council that helped me in all stages of the study and other colleagues who advised me at particular points.

Last, but not least, I would like to thank The Lord of Mount Zion and my Ancestors(Bakone, Lions of the North) for the gift of life, the gift of wonderful people I have met and re-met along this journey and granting me the strength I needed to complete my study.

Ecclesiastes 10:19 ~A feast is made for laughter, wine makes life merry but money answers all.

ABSTRACT

South African dairy cattle industry is characterized by a dual production system, comprising of a high input commercial production system and low input smallholder and emerging dairy herds. Performance data from both systems are included in national genetic evaluations, with models that assume homogeneous variances. If variances are heterogeneous, above average animals in more variable herds will be favoured over high performing animals in the less variable herds. This may result in biased selection and inaccurate estimation of breeding values. With intensified selection, genetically inferior animals could be chosen, thereby decreasing the realised genetic gain, resulting in lower productivity. The aim of the study was to investigate the extent of heterogeneity of variance between the two dairy production systems South African Holstein cattle.

Milk production data were obtained from the Integrated Registration and Genetic Information System of South Africa (INTERGIS).High input production system data set consisted of 68 000 lactation records from 741 herds, recorded between 2006 and 2018.Pedigree file comprised of 38 126 daughters of 2 472 sires and 4 305 dams. Data for the low input production system comprised of 32 388 lactation records of 3 325 daughters of 134 sires and 253 dams from 59 herds recorded from 2006 to 2018. Hartley's F_{max} test was used to test for heterogeneity of variances for 305 day yields of milk, fat and protein between the high and low input production systems. Non-genetic factors affecting these traits were then determined by the Proc GLM procedure of SAS. Genetic and phenotypic parameters among these traits were estimated, for each production system, by the Restricted Maximum Likelihood (REML) procedure in the ASREML software.

Heritability estimates for milk, fat and protein yield, respectively, were 0.70 ± 0.027, 0.55 ± 0.35 and 0.64 ± 0.03 for the low input production system compared to 0.16 ± 0.014, 0.11 ± 0.012 and 0.145 ± 0.013 for the high input production system. Estimates for genetic correlation between milk and fat, milk and protein and fat and protein were 0.68 (0.03), 0.81(0.01) and 0.81(0.02) in the high input production system and 0.80(0.34), 0.90(0.02) and 0.91(0.01) in the low input production system respectively. Phenotypic correlations in the high input dairy production system were 0.85(0.00), 0.92(0.00) and 0.88(0.00) for milk and fat, milk and protein and protein and fat and 0.82(0.08), 0.91(0.01) and 0.91(0.34) in the low input production system, respectively.

Genetic prediction models for milk production traits, in South African Holstein cattle, should account for heterogeneous variances between the high and low production systems. Herd-year-season of calving, parity and linear and quadratic effects of age at calving should be included on the models. There is a need to increase selection pressure in the low input production system, in order to improve genetic merit for milk production traits.

Table of Contents

List of tables

List of figures

List of Abbreviations

ARC	Agricultural Research Council
CV	Coefficient of Variation
DAFF	Department of Agriculture Fishery and Forestry
EBV	Estimated breeding values
FAO	Food and Agriculture Organisation
GLM	General Linear Models
HYS	Herd, year and season
HYSD	Herd-year-standard-deviation
INTERGIS	Integrated Registration and Genetic Information System
MUN	Milk Urea Nitrogen
NDAIS	National Dairy Animal Improvement Scheme.
NDARIS	National Dairy Animal Recording and Improvement Scheme
REML	Restricted Maximum Likelihood
SAS	Statistical Analysis System Software
SCC	Somatic Cell Count
Stats SA	Statistics South Africa
TMR	Total Mixed Ratio

Chapter 1 : INTRODUCTION

Low dairy cattle herd profitability is a major problem all over the world (Lactodata, 2016).Therefore, there is a need to improve dairy production efficiency and this can be largely achieved by accurate selection for economically important traits. In order to ensure reliable estimation of breeding values, and hence accurate selection, genetic evaluation models need to account for heterogeneity of variances that may exist among groups of herds. If variances are heterogeneous, above average animals in the more variable herds will be favoured over high performing animals in the less variable herds (Winkelman and Schaeffer, 1988 and Lino-Lourenço *et al*., 2012). This may result in biased selection and inaccurate estimation of breeding values (Everett *et al*., 1982; Hill, 1984; Brotherstone and Hill, 1986; Garrick and Van Vleck, 1987; Dodenhoff and Swalve, 1998). Thus, failure to adjust for such heterogeneous variances will result in inaccurate selection, which will hamper genetic progress.

The South African dairy cattle industry is characterized by a dual production system, comprising of a high input commercial production system on the one hand, and low input smallholder and emerging dairy herds on the other hand. Performance data from both systems is included in the national genetic evaluations, and the models used assume homogeneous variances. The differences in management and environmental conditions could, however, lead to heterogeneous variances between these two productions systems (Ronegard *et al.*, 2013).

Biases in selection and evaluations occur over time as dams and daughters tend to express similar records in the production environment, and may worsen over time (Vinson, 1987). When selection intensifies, this could lead to choosing animals that are not genetically the best, which may decrease the realised genetic gain (Carneiro Júnior *et al.,* 2007) and this may also present a problem when evaluating sires, if they are not randomly distributed across production systems. It is, therefore, imperative to investigate the presence of heterogeneous variances in situations where there are variable production environments, such as in South Africa. The importance of such a study is highlighted by the current economic viability problems that the South African dairy industry is facing.

Genetic parameters and environmental factors influencing milk production traits in South African dairy cattle have been reported in previous studies (Kgole *et al.*,2013 and Makgahlela *et al*.,2007). However, these reports have been on a national scale comprising mostly of the high producing herds that are characterized by elite cows and better management. Comparison of genetic parameters between the different dairy production systems of South Africa has not been conducted. It is important to estimate such parameters within these two production systems and closely monitor any differences or similarities, in order to develop sound genetic improvement programmes.

The aim of the current study was to investigate the possibility of heterogeneity of variances for milk production traits between the low and high input production systems in South Africa, identify non-genetic factors that contribute to heterogeneity of variance and to estimate genetic parameters for these traits within each production system.

The objectives of the study were:

I. Test for the existence of heterogeneity of variance for milk, fat and protein yield between the low and high input dairy cattle production systems of South Africa.

II. Determine non-genetic factors influencing variation in milk, fat and protein yield in the high and low input dairy cattle production systems of South Africa.

III. Estimate heritabilities, genetic and phenotypic correlations for milk, fat and protein yield within the low and high input dairy cattle production systems of South Africa.

The following hypotheses were tested in this study:

(i) Variances for milk, fat and protein yield between the low and high input production systems in South Africa are not heterogeneous.

(ii) There are no non-genetic influences on variation in milk, fat and protein yield in the high and low input dairy production systems of South Africa

(iii) There is no variation in genetic and phenotypic association among milk, fat and protein yield within the low and high input dairy production systems of South Africa

Chapter 2 : LITERATURE REVIEW

2.1 Introduction

This chapter presents background information on the South African Holstein breed in the two production systems and highlights the economic importance of milk production traits. Literature on factors responsible for heterogeneity of variance, environmental factors affecting milk production traits, estimates of their heritabilities as well as genetic and phenotypic correlations among milk, fat and protein yield are also reviewed. Genetic trends of these traits in different populations are discussed.

2.2 The South African dairy industry

Milk and meat producers worldwide must double their production in order to meet the demand of the exponentially growing human population (FAO, 2007). The human population globally grew by 100 million people in the year 2015 and South Africa experienced a 1.6 % population growth (Stats SA, 2018). This continuous growth in population, increase in income and dietary changes will lead continuous consumption growth.

Besides providing employment to 45 000 people and feeding 120 000 families, including the farmers and their families, the South African dairy cattle industry contributes 14.5 billion rands annually to the country's gross domestic product (Lactodata, 2017). The South African dairy industry is characterized by a dual production system, comprising of high input commercial dairy herds and low input smallholder and emerging dairy herds. The dairy industry is, therefore, important to the South African economy; hence, there is a need to ensure sustainable milk production in both the high input and low input production systems.

South Africa produces 3 253 000 tons of dairy products. The country imports 83 504 tons of dairy products and exports 48 627 tons (Lactodata, 2018). Most of the milk production in South Africa (82.74%) occurs in the coastal areas due to their mild temperatures and good rainfall ensuring the availability of good natural and planted pastures (DAFF, 2012). The Western Cape is the leading province, producing 30.6 % of the total milk produced in the country, followed by the Eastern Cape with 28.4%, Kwa-Zulu Natal 23.7 %; Free State 6.8%, North west 4.5 % with the remaining 6.1 % being produced by Limpopo, Mpumalanga, Gauteng and the Northern Cape.

The South African dairy industry is characterized by a dual production system, comprising a low input low output production system and a highly productive high input production system. The low input production system is characterized by low feeding and management levels, with herd size ranging from 2 to 50 animals. Natural pasture is the main feed source, with limited supplementation. Meanwhile, the high input production system is characterized by large herd sizes, exceeding 100, high levels of feeding and management and they are highly developed (Lactodata, 2016). The main feeding systems for dairy cattle on high-input herds are total mixed ration (TMR), supplemented pasture-based systems or a combination of both (Theron and Mostert, 2009).

2.2.1 Low input production system

Limited production information is available on the low input dairy production system, in contrast to the high input dairy production system (Abin *et al*., 2018). Efforts to improve dairy production have been in place since 1917 (Banga, 2000) through the National Dairy Animal Improvement Scheme (NDAIS). Recent policy changes to include low input dairy farmers have been implemented with the aim of improving individual cow performance and implementing herd improvement programs, as the scheme was initially exclusive to high input(commercial and stud) dairy farmers (Banga, 2000). The high input production system has been studied extensively and information on phenotypic, genotypic and economic parameters has been reported (Abin *et al*., 2018)

Abin *et al*. (2018) reported that cows in the low input production system produced significantly less ($p < 0.05$) than those in the high input production system. Average milk, fat and protein produced in the low input production system was 4097, 174 and 141 kilograms (Kg) respectively, per 305-day lactation and 6 921 kg of milk, 298 kg of fat and 60 245 kg of protein in the high input production system.

There are about two million dairy farms in the low input smallholder dairy production system (Mapekula *et al*., 2011), classified into communal and emerging farmers (Tanyanyiwa *et al*., 2016). The low input production system is characterized by small herd sizes of between 2 and 50 cows per herd and low levels of feeding and management. Farms in this production system are known to have poor recording systems and unplanned, non-synchronized mating systems. Feeding is constrained and dependent on agro-ecological factors and farmer's socio economic status. Natural forage is the main source of feeding, with little or no supplementation. Disease management is a major constraint in this sector (Abin *et al*. 2018; Mostert, 2007).

The communal farmers face challenges related to herd size, availability of feeds, technical and water resources scarcity and land disputes (Chinogaramombe *et al*., 2008) while emerging farmers are mostly affected by market prices as their main focus is to produce and sell (Senyolo, 2009). According to Moloi (2010), emerging farmers invest more in technical, feed and water resources. Farmers in this sector are continuously affected by high rates of unemployment, poverty and inequality (Thindisa, 2014; Ntshephe, 2011). They share pastures and facilities under the government land redistribution program.

Successful utilisation of high quality animal genetics has various challenges (Kariuki *et al*., 2019). These challenges are more predominant and have a greater impact on developing smallholder production systems (Madalena, 2008). Smallholder systems are the main producers of milk in developing countries (FAO, 2011). Sustainability of these systems depends on their long-term profitable productivity. Challenging production environments, coupled with limited investment capital are the main hindrances to productivity and profitability of these systems (Oosting *et al*.,2014 and

Rege *et al*., 2011). As a consequence, smallholder farms are mainly low input, which generally implies poor quality and insufficient quantities of feed, low hygiene, poor housing and animal health services; factors that result in low productivity. Unfortunately, in the face of these challenges, intensification of production has been through the introduction of high input breeds, resulting in sub-optimal performance and unprofitable dairy farming (TIAPD, 2016).

Highly specialised breeds have been performing below average in the smallholder dairy production system, which is mainly due to mismatch of genotype by environment (Wilson, 2009). This can be eradicated by environment specific breeding programs (Okeno *et al*.,2010; Rica *et al*., 2004). However, implementation of such breeding programs in the smallholder dairy production system has been hampered by limited pedigree and performance recording (Abin *et al*., 2018 and Kariuki *et al*., 2019).

2.2.2 High input production system

The highly sophisticated and technologically advanced high input production system is characterized by large herd sizes, cows exceeding 100 per herd, with high levels of feeding and management. Breeding in this production system is planned and based on production and reproduction records. In most instances artificial insemination is practised using breeder proven bulls or imported semen. The main feeding systems for dairy cattle on high-input herds are Total Mixed Ration (TMR), supplemented pasture-based systems or a combination of both (Theron and Mostert,2009).

2.3 The South African Holstein breed

Holstein is the most widely used dairy cattle breed globally and in South Africa (Banga *et al*., 2014). It has the highest average milk yield amongst the four major breeds of South Africa (Mostert, 2007; Kgole *et al*., 2013). The breed is believed to have been selected for dairy qualities for about 2000 years in Friesland, a northern province in the Netherlands. It is loved by producers for its unsurpassed milk production and adaptability to multiple production environments.

2.4 The National Dairy Animal Recording and Improvement Scheme

Individual cow performance data is routinely recorded by the National Dairy Animal Recording and Improvement Scheme. Milk yield of individual cows is recorded at each milking. Parameters measured using milk samples for each cow are fat, protein, lactose percentage, somatic cell count (SCC), and milk urea nitrogen (MUN). The data, together with pedigree data, are captured on the Integrated Registration and Genetic Information System (Intergis) and subsequently used to estimate breeding values. These breeding value (EBV) estimates are used by dairy producers for selection (SA yearbook, 2009/10).

2.5 Milk production traits

Genetic improvement of dairy cattle is primarily aimed at improving traits that are directly related to herd profitability and sustainability of milk production (Cho *et al*., 2016). Milk yield, protein yield and fat yield are among the primary traits included in dairy cattle selection objectives (Bahreini-Behzadi *et al*., 2013).

Cow milk can be regarded as one of the most nutritious agricultural products and forms a vital part of the human diet. It is therefore, widely regarded as a key contributor to improving human nutrition and food security specifically in developing countries (Aimutis, 2004; Bauman et *al*., 2006: Mandal *et al*., 2014). In addition to its nutritional and health promoting attributes, milk can be a reliable and constant source of income for poor communities in which they can use to overcome poverty and malnutrition (Hemme and Otte,2010).

Table 2.1 shows a consistent increase in average yield of milk, fat and protein despite the decrease in the number of cows. Milk, fat and protein decreased from the year 2007 to 2009, which could be attributed to draughts and global economic recession. Production records analysed were not classified on famers’ input level, the low average production might have been because of the low production in the low input production system lowering the production in the high input production system.

Table 2.1: Average 305-day production per lactation for cows participating in the National Dairy Animal Recording and Improvement Scheme from the period 2001-2011.

Year	N. of Cows	Milk (Kg)	Fat (Kg)	Protein (Kg)
2001-2002	34 603	5 275	237	192
2002-2003	35 399	5 262	244	194
2003-2004	39 093	5 455	257	202
2004-2005	31 350	5 602	260	204
2005-2006	32 748	5 806	270	208
2006-2007	30 734	5 836	273	218
2007-2008	29 091	5 745	268	217
2008-2009	33 654	5 738	266	215
2009-2010	29 004	5 799	270	214
2010-2011	28 260	5 866	275	221

Adapted from the National Dairy Animal Improvement and recording Scheme

2.6 Heterogeneity of variance for milk and component yields and its implications on dairy cattle evaluation and selection.

Genetic improvement in dairy cattle is largely dependent on accurate knowledge of phenotypic and genotypic differences among individual animals. If selection is based on inaccurate information, genetic gain is reduced. The presence of cow heterogeneous variance complicates the process of cow indexing, a procedure used to estimate a cow's breeding value by combining its own and its relatives' information.

Best linear unbiased prediction (Henderson, 1978) has been widely used in the estimation of breeding values. The procedure assumes uniformity in variances among individuals within a level of an effect. However, if variances are found to be unequal, heterogeneity of variances is said to exist. A high percentage of above average cows has been reported in high variance (Evert *et al*., 1982) and high producing herds (Powel *et al*., 1982) when variances are heterogeneous. Powel (1984) showed that if variances are heterogeneous and selection intensifies, EBVs of animals from the more variable and higher producing herds are biased upwards. The distribution of daughters may not be random among herd production and variability levels, which may lead to over-evaluation of sires that have a high percentage of their daughters in high variance herds. The existence of heterogeneous variances inflates the estimated breeding values of bulls from high producing and high variance herds (Garrick and Vleck, 1987). Heterogeneous variances give rise to problems, not only in the selection of sires, but also for potential bull-dams.

2.7 Sources of heterogeneity of variance for milk in dairy milk production

Milk yield and composition is influenced by multiple factors within the cow and its environment. Some of these factors under effective management can be manipulated in order to improve milk yield and composition while others are beyond the farmer's control. Factors that influence milk production also contribute to heterogeneity of variance amongst and within herds. These factors include herd management, year and season of calving, parity and age at calving, the interaction between reproduction and productivity traits and milking frequency and interval.

2.7.1 Herd

Herd has been found to significantly influence milk, butterfat and protein yield in South African Ayrshire and Jersey cattle (Hallowell *et al*., 1998; du Toit, van Wyk & van der Westhuizen, 1998). Kgole (2013) reported similar results for test-day production of South African Holstein cattle. Kunaka & Makuza (2005) and Mandizha, Makuza & Mhlanga (2002) also reported herd to significantly ($p<0.0001$) affect milk, butterfat and protein yield of Holstein cattle in Zimbabwe. This variation is caused by management, climatic and genetic factors (Kabunga and Agyemang, 1989) and it is also important to have an accurate knowledge of these factors (Vercoe and Frisch, 1990). According to Mosi (1984), herd effects are responsible for 30% variation in milk yield and composition.

Nutrition contributes to variation amongst herds as it affects milk yield and composition (Mackle *et al*., 1999). Heat stress can severely depress milk production (Bohmanova *et al*., 2007). Cold weather can also depress milk production as the production energy is used for body maintenance (Huquet *et al*., 2012; Hammai *et al*., 2015). Rainfall is the major climatic factor affecting production because it determines the availability and quality of both planted and natural pastures (Mbap and Ngere, 1989). These factors do not only result in decreased production but also increase the possibility of health complications such as acidosis at herd level (Zaabza *et al*., 2017). Differences in levels of supplementation and management also result in variation among herds. Variation in production traits among herds of the same breed is attributable to differences in nutrition and management practices, as well as variable environmental conditions (Kunaka & Makuza, 2005).

2.7.2 Year and season of calving

Several studies (Hallowell *et al*., 1998; du Toit, van Wyk & van der Westhuizen, 1998) have reported that calving year has a significant effect on milk production. Similar findings in South African Holstein cattle were reported by Kgole (2013). M'handi *et al*. (2012) suggested that the annual variation in milk production could be a result of changes in herd size, age of the animals and management practices.

Hot and humid seasons have a negative impact on milk composition, especially fat (Bernabucci *et al*., 2002; Rhoads *et al*., 2009). Cows calving in winter or autumn produce more milk than those calving in spring or summer (M'hamdi *et al*., 2012). Albarran-portilo and Pollott (2011) found that cows that calved during summer and autumn lactate longer than those that calved in winter and spring. Boualloge *et al*. (2013) reported that the lowest level of production is found in cows that calve during summer and that these cows are more persistent. South African Holstein cattle that calved in winter had 186 kg more milk than those that calved in summer (Mostert *et al*. 2001). Above average environmental temperatures have been found to depress both fat (Jennes, 1985) and protein yield (Keown, 1986). The availability and quality of pasture is mainly dependent on rainfall, which is never consistent from year to year and season to season.

2.7.3 Parity and age at calving

Several researchers have reported that parity has a significant effect on milk production traits (Mohsen *et al*., 1999; Bajwa *et al*., 2004; M’handi *et al*., 2012; Nyamushamba *et al*., 2014; Petrovic *et al*., 2015). The South African Holstein was found to have the lowest milk yield in the first parity and the highest in the third party (Makgahlela *et al*., 2007; Kgole *et al*., 2013). Milk, fat and protein yield increase with parity up-to a peak, then they decrease gradually in later parities (M’handi *et al*., 2012; Kunaka and Makuza, 2005; Nyamushamba *et al*., 2014; Mosi, 1984). The effect of parity on milk, fat and protein yield maybe due to changes in management and environmental conditions among parities (M’handi, 2012).

Milk production in heifers is limited by their need for energy for growth, as well as underdevelopment of the udder and mammary gland in younger tissues. Production by age at calving follows the same trend as parity, which increases to a peak as the cow advances to maturity and then declines gradually as the cow ages and its ability to efficiently utilize nutrients and general metabolism decreases. Age at calving was found to have a significant effect on milk, butterfat and protein yield in South African Ayrshire and Jersey cattle breeds (Du toit *et al*., 1998; Howell *et al*., 1998). Mostert *et al*. (2001) also reported a significant effect of age at calving on milk, butterfat and protein yields in South African Holstein and Jersey cattle.

2.8 Genetic parameters.

Development of animal breeding plans requires knowledge of heritability, repeatability and phenotypic and genotypic correlations of the traits included. These parameters are needed to evaluate the breeding plan itself as well as to predict breeding values of the animal. Genetic parameters are descriptors of the populations they are predicted from and may change over time. These parameters are specific to a particular group and environment.

2.8.1 Heritability

Heritability is a concept that summarizes how much of the variation in a trait is due to variation in genetic factors (ratio of additive genetic variance to phenotypic variance). It is often used in reference between parents and their offspring with regard to a specific trait. High heritability implies that there is strong resemblance between parents and offspring, while low heritability implies a low level of resemblance (Wray and Vissicher, 2008).

Estimating heritability for desired traits and using heritability to calculate breeding values is one important step in speeding up selection response (Rege *et al*.,1992). Estimation of genotypic and phenotypic parameters has, however, presented serious difficulties due to the lack of reliable periodic production records for the important traits of economic importance in the low input production system (Abin *et al*., 2018). As a consequence selection decision according to the needs and conditions for the specific production system face great uncertainty, more especially for young bulls and cows (Everechii *et al*.,2011).

Table 2.2: Heritability estimates for milk, fat and protein in different production level as reported in literature

Herd production level	Milk	Fat	Protein	Reference
Low	0.12	0.12	0.09	Logar *et al*.,(2007)
High	0.22	0.19	0.18	
Low	0.30	0.23		Costa,(1999)
High	0.22	0.20		
Low (Brazil)	0.29			Ceŕon-Munoz *et al.,*(2004)
High (Brazil)	0.37			
Low(Columbia)	0.28			
High(Columbia)	0.27			
Low	0.15			Muasya *et al.,*(2007)
Medium	0.22			
High	0.31			
All	0.26	0.149	0.238	Toghiani, (2012)

Heritability estimates for milk production traits were low (Table 2.2) in the low herd-year-standard-deviation (HYSD) groups, except for those reported by Ceŕon-Munoz *et al.*(2004), this could be attributed to the low selection pressure in the high HYSD groups (Banga, 1992). Protein had the lowest heritability estimates, followed by fat yield while milk yield had the highest heritability estimates. Heritability estimates for milk yield are increasing over time with the production level with fat and protein following suit. The heritability for protein in the high herd year standard deviation was twice the heritability in the low HYSD. The lowest heritability reported was 0.09 for protein (Logar *et al*.,2007) and the highest was milk at 0.37 (Ceŕon-Munoz *et al.,* 2004).Similar findings of Heritabilities increasing with production level have been reported in the Rendena breed (Guzzo *et al*., 2018) and in sheep (Nikolau *et al*., 2004).

2.8.2 Phenotypic and genotypic correlations

Phenotypic and genotypic correlations are considered as raw materials in planning a sound and practical breeding plan and genetic evaluation (Ruales *et al*., 2007). Correlations play a vital role in multiple-trait analysis; they are used to measure the extent at which one gene or trait influences the performance of multiple traits at the same time (Kekana, 2018). They can be used to select and evaluate multiple traits at the same time while using only one of the traits (Missanjo *et al*., 2013). They are necessary to determine the degree of (co)variation due to genetics and the environment (Rincon *et al*., 2015) and provide an indication of the extent of association between traits (Van Alfren, 2014). Economically important traits may be correlated in domesticated animals, and the extent of their association can be predicted by genetic correlation (Albuquere *et al*., 1991).

Lack of recording of both phenotypic and pedigree data in the South African smallholder system poses a serious problem to genetic improvement. Production and reproduction records in this extensive system are virtually non-existent and measuring of basic traits is a problem due to limted infrastructure (Goofy *et al*., 2018). On the other hand, much progress in dairy genetic evaluation has been made in the commercial sector in the past three decades, making it possible to select animals of high genetic merit to contribute to genetic progress (Koster *et al*., 2018.).

Table 2.3: Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations among milk, fat and protein yield in three parity levels according to literature

Parity	Trait	Milk	Fat	Protein	Reference
1	Milk		0.62	0,89	Kgole *et al.*,(2013)
	Fat	0.72		0.61	
	Protein	0.87	0.75		
2	Milk		0.66	0.91	
	Fat	0.72		0.66	
	Protein	0.89	0.79		
3	Milk		0.67	0.91	
	Fat	0.72		0.67	
	Protein	0.89	0.78		
1	Milk		0.92	0.92	Mandizha *et al.*,(2002)
	Fat	0.92		0.88	
	Protein	0.95	0.92		
2	Milk		0.86	0.93	
	Fat	0.89		0.88	
	Protein	0.97	0.92		
3	Milk		0.83	0.93	
	Fat	0.92		0.93	
	Protein	0.98	0.94		
1	Milk		0.39	0.86	Wasana *et al.*, (2015)
	Fat	0.66		0.73	
	Protein	0.91	0.56		
2	Milk		0.81	0.51	
	Fat	0.91		0.73	
	Protein	0.66	0.68		
3	Milk		0.78	0.74	
	Fat	0.65		0.73	
	Protein	0.91	0.52		

Table 2.4: Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations among milk, fat and protein yield in all parity levels according to literature.

Source	Trait	Milk	Fat	Protein	Reference
1	Milk		0.81(0.01)	0.94(0.01)	Zaazba *et al*., (2017)
	Fat	0.82(0.01)		0.86(0.01)	
	Protein	0.95(0.02)	0.85(0.03)		
2	Milk		0.81	0.70	Toghiani, (2012)
	Fat	0.44		0.705	
	Protein	0.76	0.68		
3	Milk		0.72	0.89	Tesfa *et al*., (2004)
	Fat	0.78		0.85	
	Protein	0.94	0.85		
4	Milk		0.77	0.89	Lui *et al*.,(2014)
	Fat	0.82		0.85	
	Protein	0.95	0.83		
5	Milk		-0.28(0.190)	-0.40(0.137)	Rincòn *et al*.,(2015)
	Fat	-0.11(0.014)		0.42(0.010)	
	Protein	-0.22(0.013)	0.82(0.126)		
6	Milk		0.931(0.04)	0.931(0.04)	Zaazba *et al*., (2016)
	Fat	0.946(0.05)		0.971(0.05)	
	Protein	0.56(0.05)	0.957(0.06)		

The genotypic correlations were positive and high (Table 2.3 and Table 2.4), indicating that selection for one trait will positively affect other traits. Rincòn *et al*. (2015) reported low genetic correlation between fat and protein and negative phenotypic correlations between milk and fat, milk and protein which could have negative implications if some of the traits are not included in the selection objective. Genotypic correlation among milk, fat and protein in South African Holstein cattle were reported to be positive and high by Tesfa *et al*. (2004) and moderate to high in another study by Kgole *et al.* (2013), this estimates reported were from animals in the high input dairy production system.

Genetic and phenotypic correlations between milk, fat and protein reported in literature were generally moderate to high and positive. This can assist in improving accuracy of genetic evaluations, in multi-trait models including these traits.

2.9 Genetic trends

Traits that are directly related to herd profitability have been a great deal of interest to breeders (Essl, 1998). For proper genetic improvement of such traits, there is a need to routinely evaluate them and track their progress in order to make adjustments aimed at optimising genetic gain, which increases profitability (Flemming *et al*.,2018). This can be achieved by assessing genetic trends over time, which evaluates the changes brought by the selection process.

Genetic trend is the change in performance per unit of time, due to changes in mean breeding value. Understanding of genetic trends will not only help farmers to establish future genetic direction looking at specific goals for breeding a profitable and sustainable herd, but also in comparing alternative methods for genetic improvement (Javed *et al*., 2007).

The number of officially recorded traits have significantly increased along with their calculated EBV's. Estimated breeding values for more than 20 traits for major dairy breeds are being routinely published (Ramatsoma *et al*., 2014). Increased selection intensities for milk production traits in the South African dairy industry have resulted in an increase in genetic trends of these traits (National Dairy Animal Recording and Improvement Scheme, 2011). Given the availability of EBVs for these traits and the potential for selection towards the implementation of favourable genetic trends, strategies are needed to continually improve the genetic prediction models in order to maximise rates of genetic gain in South African Holstein dairy cattle (Ramatsoma *et al*., 2014).

2.10 Conclusion

Holstein is the most widely used dairy cattle breed in South Africa, due to its high production potential and ability to adapt to various production environments. Milk, fat and protein yield are among the most economically important dairy production traits. It is important to test for heterogeneous variances for these traits between the high and low input production systems of South Africa, in order to avoid biases in genetic evaluation. This will contribute towards more accurate selection, leading to increased rates of genetic gain and more efficient dairy production. Accurate knowledge of phenotypic and genotypic variances is necessary for the estimation breeding values for Holstein cattle, in the major production systems in South Africa. Estimates for heritability for milk, fat and protein yield have been reported to be generally moderate to high in literature. Genetic and phenotypic correlations among these traits have been found to be high and positive in most studies. Genetic trends for South African Holstein dairy cattle breed have been reported to be positive in previous studies.

Chapter 3 : MATERIALS AND METHODS

3.1 DATA

Data for the high and low input dairy cattle production systems were obtained from the Integrated Registration and Genetic Information System of South Africa (INTERGIS).

The original data set for the high input dairy Holstein cattle production system consisted of 4 541 908 cow lactation records of 161 8579 animals from 8 845 herds collected between 1902 and 2018. The pedigree file comprised of 2 534 111 cows, daughters of 17 131 sires and 937 973 dams. For the low input dairy Holstein cattle production system, data comprised of 65 790 lactation records of 3 326 animals from 70 herds recorded from 2006 to 2018. The low input production system pedigree file consisted of 3 325 daughters of 134 sires and 253 dams from 59 herds.

The data sets were edited using the Statistical Analysis System Software (SAS, 2013), where the following basic edits were carried out for both data sets.

I. Removal of records with missing information (e.g. herd identification, birth date, calving date or lactation number).
II. Removal of outliers for 305-day milk, fat and protein yield, according to the standards used in the national genetic evaluation system (Mostert *et al*., 2006).
III. Restricting parity to fall within the following ranges: 20 – 34, 30 – 54 and 40 – 66 for parity one, two and three, respectively, following Mostert *et al*. (2006). Calving seasons were defined as wet (October – March) and dry (April – September) (Dube, 2006).
IV. Removal of calving records with calving dates before 2006.
V. Herd, year and season of calving were concatenated to create herd-year-season contemporary groups.

The pedigree file for each production system was built around animals from the final edited data set, going three generations back. The final pedigree consisted of animals with known sires, dams and birth dates. For the high input production system, the pedigree was made up of 42 727 animals from 2 605 sires and 33 822 dams, and for the low input production system it consisted of 2 128 daughters of 95 sires and 180 dams.

3.2 Statistical analysis

3.2.1 Test for heterogeneity

The F_{max} procedure of SAS (SAS, 2013) was used to test the assumption of uniform variances.

Variance components were tested using:

$$F_{max} = \frac{s^2 \text{ largest}}{s^2 \text{ smallest}}$$

Where,

s^2 Largest is the largest of the group variances,

s^2 Smallest is the smallest of the group variances.

3.2.2 Non-genetic factors influencing milk production traits.

The General Linear Models (GLM) procedure of SAS (SAS, 2013) was used to determine non- genetic factors that influence variation in milk production traits in the two dairy production systems separately. These factors included herd-year-season of calving, quadratic and linear effects of age at calving. The following model was fitted:

$$Y_{ijk} = \mu + HYS_i + \beta_1(AC) + \beta_2(AC^2) + P_j + e_{ijk}$$

Y_{ijk} is an observation of 305-day yield of milk, fat or protein

μ is the overall mean,

HYS_i is the fixed effect of the i^{th} herd-year-season of calving,

β_1 and β_2 are, regression coefficients for linear and quadratic effects of age at calving respectively,

AC and AC^2 are the linear and quadratic effects age at calving

P_j is the j^{th} fixed effect of parity (j = 1, 2, 3)

e_{ijk} is the random residual error, assumed to be independent and normally distributed with mean 0 and a uniform variance *i.e.: N* ~ $(0, I\sigma_e^2)$.

3.2.3 Estimation of genetic parameters

The Restricted Maximum Likelihood (REML) procedure was used to estimate variance and covariance components for milk, butterfat and protein yield, using the ASReml software (Gilmour *et al*., 2001).

Two methods were used to estimate (co)variance components for milk, butterfat and protein yield. These variance components were estimated from a multi-trait animal model, using the following mixed model equations.

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

Where $Y_{1,}$ Y_2 and Y_3 are the vectors of observations for milk production traits (305-day milk, fat or protein yield)

$X_{1,}$ X_2 and X_3 are incidence matrices relating observations to fixed effects.

$b_{1,}$ b_2 and b_3 are vectors of fixed effects influencing milk production traits.

Z_1, Z_2 and Z_3 are incidence matrices relating random animal additive genetic effects to observations.

u_1, u_2 and u_3 are vectors of random animal additive genetic effects

e_1, e_2 and e_3 are vectors of random residual effects

The random animal additive genetic effects (U) were assumed to have a normal distribution

$N \sim (0, A\ \sigma^2_a)$ where A is the additive genetic relationship matrix and σ^2_a is the additive animal genetic variance. Residual effects (e) were also assumed to be randomly distributed with $N \sim \left(0, I\sigma^2_e\right)$, where I is the identity matrix and σ^2_e is the residual variance

The (co)variance structure for random effects was assumed to be as:

$$\mathrm{var}\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

Heritabilities were estimated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

Where:

h^2 is the heritability estimate

σ^2_a is the additive genetic effects;

σ^2_p is phenotypic variance

The phenotypic and genotypic correlations amongst traits were calculated as follows:

$$r_g = \frac{\sigma_{g_{xy}}}{\sigma_{g_x}\sigma_{g_y}}$$

Where,

r_g is the estimate of the genotypic correlation between traits x and y,

$\sigma_{g_{xy}}$ is the genotypic covariance between traits x and y

σ_{g_x} is the genotypic standard deviation for trait x

σ_{g_y} is the genotypic standard deviation for trait y

$$r_p = \frac{\sigma_{p_{xy}}}{\sigma_{p_x}\sigma_{p_y}}$$

Where,

r_p is the estimate of the phenotypic correlation between trait x and y,

$\sigma_{p_{xy}}$ is the phenotypic covariance between traits x and y

σ_{p_x} is the phenotypic standard deviation for trait x

σ_{p_y} is the phenotypic standard deviation for trait y

Chapter 4 : RESULTS

4.1 Descriptive statistics

Descriptive statistics for milk, fat and protein yield in the low-input and high input production systems are shown below in Tables 4.1 and 4.2, respectively. The means and standard deviations for milk, fat and protein yields are relatively higher in the high input production system, as compared to the low input production system.

Table 4.1: Descriptive statistics for 305-day milk, fat and protein yield (Kg) in low input production system

PARITY	TRAIT	N	MEAN	MIN	MAX	SD	CV
1	MILK	9 461	4125	527	9629	1796	43.53
	FAT	9 461	166.60	27.23	372.97	67.87	40.73
	PROTEIN	9 461	135.78	19.25	307.23	56.27	41.44
2	MILK	12 031	4068	520	9582	1755	43.14
	FAT	12 031	165.62	30.89	369.21	65.94	39.81
	PROTEIN	12 031	135.31	23.69	299.66	54.91	40.58
3	MILK	10 896	4194	507	9632	1664	39.65
	FAT	10 896	169.66	31.20	371.83	61.05	35.98
	PROTEIN	10 896	138.18	23.71	307.44	51.02	36.92
ALL	MILK	32 388	4127	507	9632	1738	42.11
	FAT	32 388	167.26	27.23	372.97	64.94	38.83
	PROTEIN	32 388	136.41	19.25	307.44	54.05	39.60

Table 4.2: Descriptive statistics for 305-day milk, fat and protein yield (Kg) in high input production system

PARITY	TRAIT	N	MEAN	MIN	MAX	SD	CV
1	MILK	28 895	7829.39	1265	14240	2495.75	31.87
	FAT	28 895	297.99	64.08	527.17	87.68	29.42
	PROTEIN	28 895	253.00	47.44	454.65	77.33	30.56
2	MILK	23 076	8299	1081	14239	2481.95	29.90
	FAT	23 076	317.96	50.64	527.12	86.65	27.25
	PROTEIN	23 076	269.64	35.53	454.30	76.36	28.32
3	MILK	16 029	8398.32	1370	14235	2392.38	28.40
	FAT	16 029	317.96	66.60	527.10	83.72	25.92
	PROTEIN	16 029	269.64	45.31	454.20	73.07	26.92
ALL	MILK	68 000	8123	1081	14 240	2480	30.53
	FAT	68 000	310.65	50.64	527.17	87.11	28.04
	PROTEIN	68 000	262.97	35.53	454.30	76.49	29.08

4.2 Test for heterogeneity

The F_{max} statistical test revealed that the variances (Table 4.3) were statistically different ($p < 0.05$) between the high and low input production systems. F_{max} values for milk, fat and protein tested at a significant level of $p < 0.05$ were 1.49, 1.77 and 1.65, respectively. These results indicate that there is heteroscedasticity for variance components for milk, fat and protein.

Table 4.3: Estimates of phenotypic variances for milk, fat and protein yield in their production environment.

Trait	Production level	variance	F_{max}	p value
Milk	High	1684400	1.49	< 0.05
	Low	1123600		
Fat	High	2016.5	1.77	< 0.05
	Low	1134.50		
Protein	High	1521	1.65	< 0.05
	Low	919.78		

4.3 Factors influencing milk, fat and protein yield

Results from the analysis of variance on the non-genetic factors influencing milk, fat and protein yield for the low and high input production systems are presented in Table 4.3. The coefficient of determination ranged from 0.76 to 0.80 in both production systems. Herd, year and season (HYS) of calving was highly significant in both production systems, for all the traits. Parity was also highly significant in both systems at (*$p<0.01$*) but the level of significance for fat (*$p<0.05$*) and protein (*$p<0.03$*) declined greatly due to the quadratic effects of age in the low input production system. The linear and quadratic effects of age were significant (*$p<.01$*) for all traits in both production systems. All non-significant factors were removed.

Table 4.4: Non-genetic factors influencing milk production traits in the low and high input production systems.

Production System	**Trait**	**HYS**	**Age**	**Age^2**	**Parity**	**R^2**
High input	Milk	***	***	***	***	0.76
	Fat	***	***	***	***	0.76
	Protein	***	***	***	***	0.77
Low input	Milk	***	***	***	***	0.77
	Fat	***	***	***	*	0.80
	Protein	***	***	***	**	0.79

***Highly Significant ($p<0.001$); **Highly Significant ($p<0.01$); *Significant ($p<0.05$);
R^2 coefficient of determination.

4.4 Heritability estimates

Estimates of heritability (Table 4.5) were high in the low input production system 0.70(0.027), 0.55(0.35) and 0.64(0.03) for milk, fat and protein, respectively. On the other hand, Heritabilities in the high input production system were relatively low 0.16(0.014), 0.11(0.012) and 0.14(0.013) for milk, fat and protein respectively.

Table 4.5: Heritability estimates for milk, fat and protein yield in the low and high input production systems

PRODUCTION SYSTEM	TRAIT	HERITABILITY (SE)
HIGH INPUT	MILK	0.16 ± 0.014
	FAT	0.11 ± 0.012
	PROTEIN	0.14 ± 0.013
LOW INPUT	MILK	0.70 ± 0.02
	FAT	0.55 ± 0.34
	PROTEIN	0.64 ± 0.03

4.5 Genetic and phenotypic correlations

Genetic correlations were high and positive in both production systems (Tables 4.5 and 4.6). The lowest genetic correlation observed (0.68 ± 0.03) was between milk and fat in the high input production system (Table 4.7) and highest (0.91 ± 0.01) was between fat and protein in the low input production system (Table 4.6). The lowest phenotypic correlation was between milk and fat (0.82 ± 0.08) in the low input production system (Table 4.6) and the highest was between milk and protein (0.92 ± 0.00) in the low input production system (Table 4.6).

Table 4.6: Genetic correlations (above diagonal), phenotypic correlations (below diagonal) and standard errors among milk, butterfat and protein yield for South African Holstein cattle in the low input production system

	MILK	FAT	PROTEIN
MILK		0.80 ± 0.34	0.90 ± 0.02
FAT	0.82 ± 0.08		0.9151 ± 0.01
PROTEIN	0.9154± 0.01	0.9152 ± 0.31	

Table 4.7: Genetic correlations (above diagonal), phenotypic correlations (below diagonal) and standard errors among milk, butterfat and protein yield for South African Holstein cattle in the high input production system.

	MILK	FAT	PROTEIN
MILK		0.68 ± 0.03	0.81 ± 0.01
FAT	0.85 ± 0.00		0.81 ± 0.02
PROTEIN	0.92 ± 0.00	0.88 ± 0.00	

4.6 GENETIC TRENDS

Genetic trends for milk, fat and protein yield in the low and high input production systems, for the period 1993 to 2013 and 1993-2016 respectively, are shown in Figures 4.1 to 4.6. Years prior to 1993 were excluded due to the extremely low numbers of records used to calculate the means.

4.6.1 Milk yield

Average EBV for milk yield in the high input production increased steadily; however there was a steep decrease between the years 2001 and 2003 and shallow drops in the years 2007, 2009 and 2014 (Figure 4.1), however milk yield increased steadily without any decline(Figure 7.1). EBV for Milk yield in the low input production system showed a downward trend; however, a rapid and visible growth was observed in the years 1995 and 2007 (Figure 4.2). Milk yield (Figure 7.2) showed a constant decline throughout the years which may be due the decline in the number of herds.

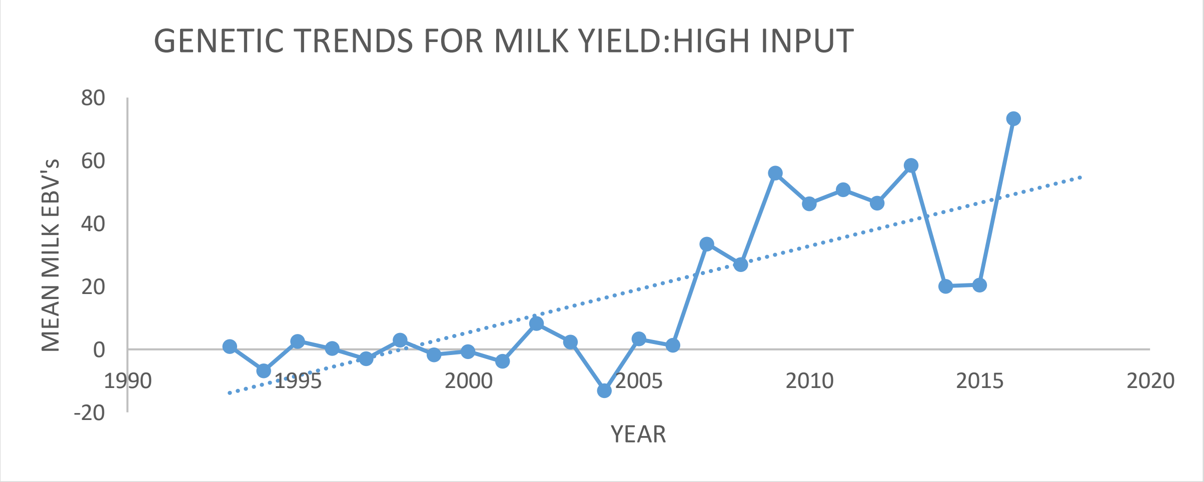

Figure 4.1: Genetic trends for milk yield in the high input production system.

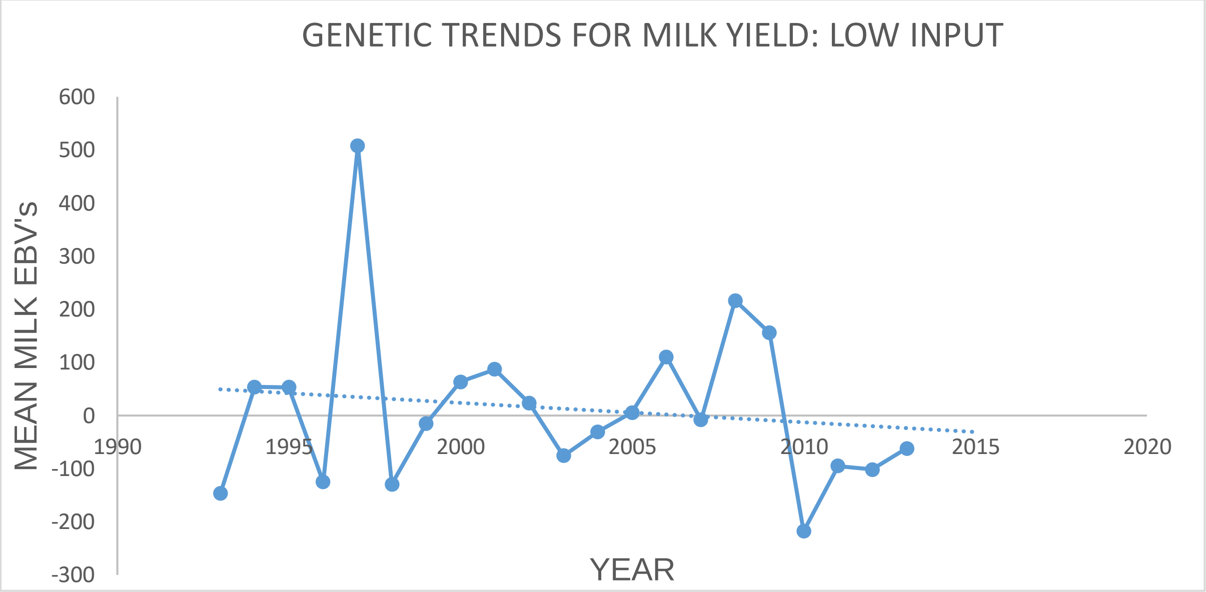

Figure 4.2: Genetic trends for milk yield in the low input production system.

4.6.2 Fat

Average EBV for fat yield and fat yield increased in the high input production system; however there was a sharp decrease from the year 2003 to 2007, with the year 2005 standing out, and deep decrease during the years 2015-2016 (Figure 4.3 and Figure 7.3). On the other hand, the low input production system showed stability for a decade in yield an EBV (2000 – 2010), followed by a steep decrease in EBV the next 3 years however the yield increased sharply in the same period (Figure 4.4 and Figure 7.4).

Figure 4.3: Genetic trends for fat yield in the high input production system.

Figure 4.4: Genetic trends for fat yield in the low input production system.

4.6.3 PROTEIN

Genetic trends for protein for followed exactly the same trend as for fat (Figure 4.5). Genetic merit for protein yield in the high input production system was positive from the year 1993 to 2016 except for few outliers (1995, 2000 and 2005). In the low input production system, it followed the same trend as milk and fat. Fat production was directly proportional to the EBV in both dairy production systems (see Appendix C)

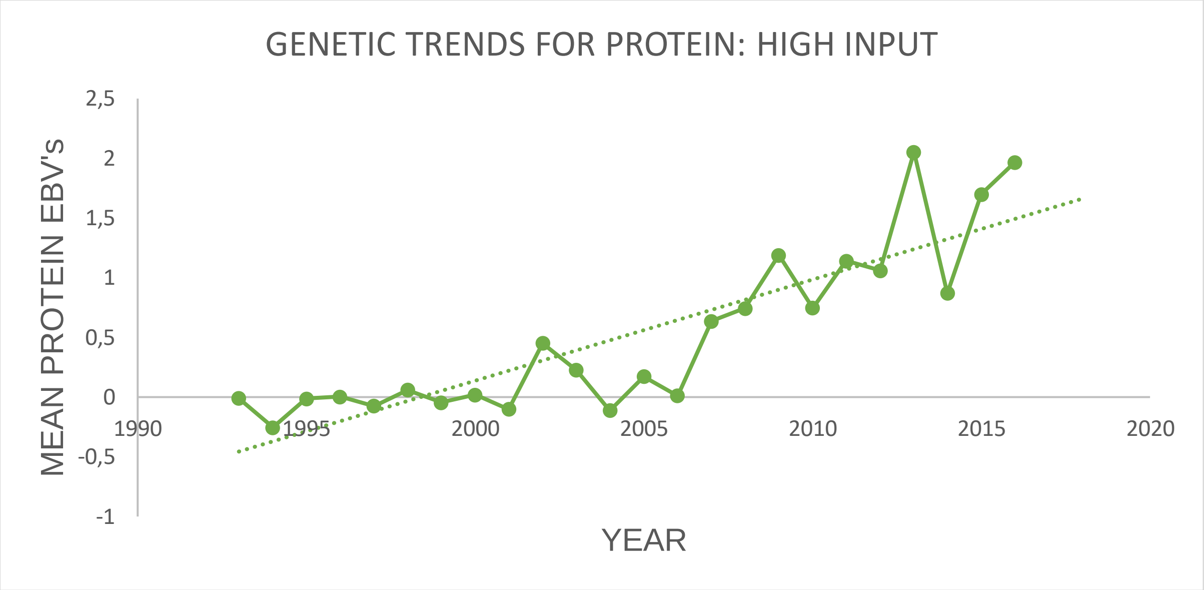

Figure 4.5: Genetic trends for protein yield in the high input production system.

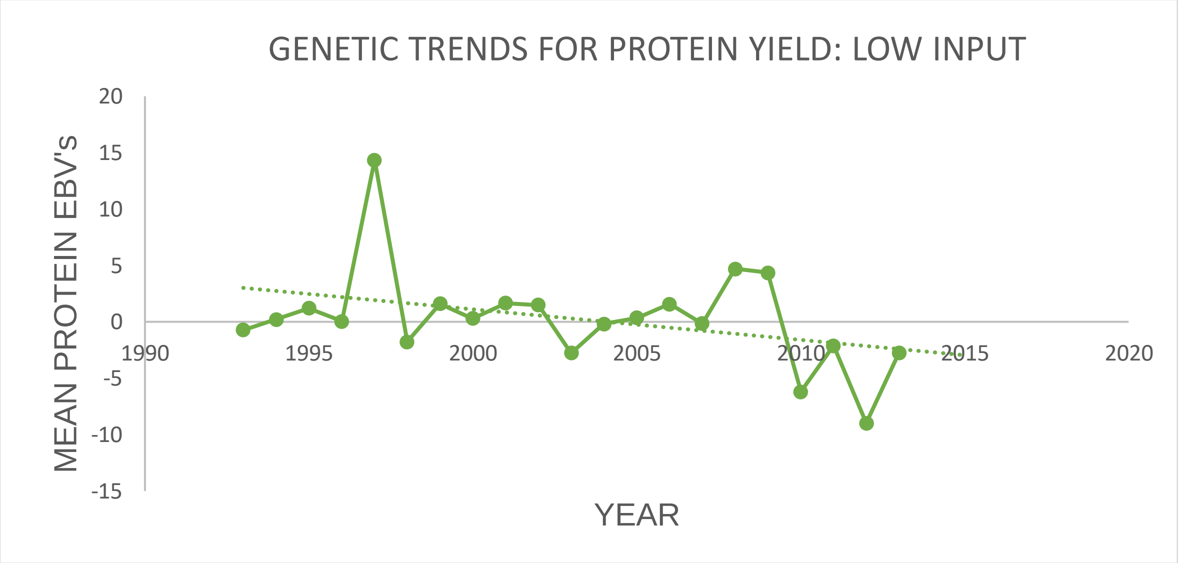

Figure 4.6: Genetic trends for protein yield in the low input production system.

Chapter 5 : DISCUSSION

5.1 Introduction

The primary aim of the current study was to test for the existence of heterogeneity of variances for dairy production traits (milk, fat and protein yield) between the high and low input dairy production systems in South African Holstein cattle. In addition, non-genetic factors influencing these traits, which may contribute to heterogeneity of variances were determined. Estimates of genetic parameters were computed for each of the two production systems. These genetic and non-genetic factors play an essential role in developing sound genetic evaluation models. This chapter presents a discussion of the findings described in the preceding chapter and attempts to put these results into perspective.

5.2 Level and variation of milk production traits.

The mean milk, fat and protein yields obtained in this study are consistent with those reported in previous studies on South African dairy Holstein cattle (Banga *et al.*, 2014; Kgole *et al.*, 2013; Makgahlela *et al*., 2006; Mostert *et al.*, 2006). The different yields are a reflection of the diverse genetics and management practices in the two production systems.

Estimates of variance components obtained in this study for milk production traits agree with those reported for Holstein cattle under comparable environments (Dodenholf and Swalve, 1998; Costa, 2000; Muaysa *et al*., 2007, Abin *et al*., 2018; Ceron-munoz *et al.*, 2004).

5.3 Heterogeneity of variance

The disparity in means, standard-deviation (SD) and coefficient of variation (CV) for milk production traits, between the two production systems, point to the possible existence of heterogeneous variances. This is confirmed by the significant test for heterogeneity of variances. The standard deviation increased with the mean for the respective trait, which was expected and has been reported in previous studies (Olukoye *et al*., 1994; Costa *et al.,* 1998; Muasya *et al*., 2007 and Guzzo *et al*., 2018). Heterogeneity of variances between the two production systems may be explained by both genetic and non-genetic factors.

5.4 Sources of variation in milk production traits

5.4.1 Herd, year and season of calving

Herd-year-season of calving was the contemporary group used in the current study and had a significant influence on milk production traits. A contemporary group can be defined as a group of animals under similar environmental conditions (Nilforooshan, 2010). Herd contributes significantly to total variation in milk production, mainly due to variability in feeding and management.

There was a significant effect of year of calving on milk production traits; which concurs with heterogeneity of variance among herd-year groups observed by Costa *et al*., (2000). The differences in production levels between years may be due to fluctuations in feed levels, rainfall, herd genetic levels and management practices and personnel.

Milk production is sensitive to seasonal variation and feed supply. Cows tend to eat less during hot and humid weather, which causes a lowering in production. Thus, summer calvers produces less than winter calvers. Cows that calved during the late dry season may produce more due to the availability of forage in the subsequent season, when they reach peak production.

5.4.2 Parity and Age at calving

Parity significantly influenced milk production. The increase in milk yield from first to third parity may be due to the differential partitioning of nutrients by first calf heifers (Olukoye *et al*., 1994). First calf heifers need nutrients for growth, maintenance and lactation, whereas older cows only require nutrients for maintenance and lactation.

The highest observed increase in 305-day milk production was between the second and third parity. This is particularly due to physiological maturity of the cow relative to the heifer, which results in a reduction in energy requirements for growth.

Milk production increases with age of the cow, reaching peak in the 4th to 5th lactation (Anderson,1985; M'hamdi *et al*,. 2012; Torshiz, 2016). This could be due in part to underdevelopment of the udder and mammary gland tissues in younger cows (Kekana, 2018).The effects of age at calving has been reported to be more significant in early parities, compared to later parities (Syrstad, 1965 and Mosi, 1984). However, Mostert *et al*. (2001) found that age class contributed the most to variation in milk, fat and protein yield in South African Holstein and Jersey cattle.

5.5 Genetic parameters

5.5.1 Variance components and heritability estimates.

Variances for milk, fat and protein yield were higher for the high input production system (Table 4.4), which compares favourably with the results found in Brazilian Holstein cattle (Costa *et al*., 1999) and in the Colombian Holstein cattle population (Cerón-Muñoz *et al*., 2004). Higher variances, however, do not translate to higher heritability estimates, as observed by Cerón-Muñoz *et al*. (2004) in Brazilian dairy Holstein cattle population.

Different herd structures and management practices have been found to be associated with heterogeneity of variances (Weigel *et al.*, 1993). Larger herd size and greater herd average yield were associated with larger variances for milk production traits (Přibyl & Pribylova, 2001). Larger herds normally adopt management practices that are appropriate for high producing dairy cows such as use of additives and concentrates to supplement forage, grouping of milking cows, veterinary programs, mastitis control and sire selection (Tong *et al.*, 1976 and Wiggans and Van Vleck, 1978;).

In South Africa, milk is produced on large intensive dairy farms as well as in small communal and emerging systems. The average number of herds used in this study shows that herds within the high input production system (Table 4.2) are larger than those in the low input production system (Table 4.1).Available resources and management practices in the high input production system may be responsible for above average performance. Herds in the low input production system are those with limited resources or less favourable management practices, which restricts the genetic expression of performance traits. In this case, average production as well as variance are depressed compared to herds in the high input production system.

Heritability is one of the most important concepts in animal breeding. It measures the strength of the relationship between the phenotype and breeding value of an individual animal. It plays a pivotal in the planning of breeding programs, estimation of breeding values of individual animals, as well as prediction of response to selection. Heritability estimates for milk, fat and protein yields were larger for herds in the low input than in the high input production system. These results follow the same trend as those reported by Costa *et al*. (1999) and (Cerón-Muñoz *et al*., 2004) and may have important implications in making decisions about breeding strategies. Heritability estimates for milk, fat and protein yield obtained in the high input production system are in the range reported by Mostert *et al.* (2006), for the same population, using fixed regression test-day models.

Heritability estimates in the low input production system resemble those found by Nauta *et al*., (2006) for organic farmers in the Netherlands. The high heritability estimates observed in this production system suggest large genetic variation, which may be due to use of cows from diverse genetic backgrounds and low production records.

The accuracy of heritability estimates is largely dependent on the quality and quantity of phenotypic records and pedigree information used. Estimates of heritability for a particular trait can differ among populations and may change over time. This, in addition to the different micro-environmental factors influencing records and models used, may explain the disparity of estimates among production systems. The lower heritability estimates obtained in the high input production system may be attributable to high selection pressure or widespread use of common sires.

5.5.2 Genetic and phenotypic correlations

Genetic and phenotypic correlations among milk, fat and protein yield were estimated to determine how these traits are associated within each of the two production systems. These parameters are required for the estimation of breeding values, which will assist in the accurate selection of animals for these traits through multi-trait genetic analysis (Van Alfen, 2014).

Estimates of genetic and phenotypic correlation for milk, fat and protein yields were relatively high and favourable in both production systems, as widely reported in previous studies (Harris & Freeman, 1992; Lembeye *et al*., 2016; Lui *et al*., 2014; Sneddon *et al*., 2016 and Tesfa *et al*., 2004).

Estimates of genetic correlation in this study (0.61 to 0.91), are similar to those reported by Kgole (2013) for South African dairy Holstein cattle using a repeatability test-day model, while the phenotypic correlations (0.83 to 0.98) are comparable to those obtained by Mandizha *et al.* (2002) in Zimbabwean Holstein cattle. The current estimates follow the same trend as those reported by Guzzo *et al*., (2018).

The high degree of association among milk production traits implies that selection for one of the traits could be used as a selection criterion for a correlated improvement in the other traits. This may also imply that the same set of genes could be responsible for the expression of these traits, which could be due to pleiotropy or linkage disequilibrium (Falconer, 1989). Pleiotropy occurs when one locus affects more than one trait, and is the main cause of genetic correlation between traits in an outbred population. Linkage is a non-random relationship between the alleles present at two or more loci (Schrooten *et al.*, 2004). Linkage between loci (or between genetic elements within genes), contributes to genetic correlations due to the fact that these linked effects tend to be inherited together.

5.5.3 Genetic trends

The genetic trends for milk, butterfat and protein yield were determined to assess the genetic progress for milk production traits in the South African Holstein cattle population. Such information helps in determining strategies for improving breeding programmes. The breeding value (BV), which is defined as the animal's individual genetic value as a parent, is very important in a breeding program and is used to select genetically superior animals for breeding. Consistent and accurate selection of animals with the best breeding values to be parents of the next generation maximizes the rate of genetic change.

A remarkable increase in the genetic merit for milk, fat and protein yield has been observed in South African dairy cattle breeds, over the past few decades (National Dairy Animal Recording and Improvement Scheme, 2001; National Dairy Animal Recording and Improvement Scheme, 2007 ; Mostert, 2007). A favourable trend observed in the high input production system indicates improvement of these traits in the population over time, which may be attributed to accurate selection decisions. However, the opposite was achieved in the low input production system.The mean breeding value over the years has generally remained stagnant, a reflection of inefficient selection and mating strategies (Rege and Mosi 1989; Ojango and Pollot 2001). The production environment may not be large enough to sustain sufficient genetic diversity and selection intensity, and inbreeding might occur over time.

Chapter 6 : CONCLUSIONS AND RECOMMENDATIONS

Significant heterogeneity of variance for milk, fat and protein yield of South African Holstein exists between the high and low input dairy production systems. It should therefore be accounted for in models for genetic evaluation of South African Holstein cattle. Differences in production between the two production systems, which is the probable cause of heterogeneous variances, may be attributable to genetic and environmental factors. A study to determine appropriate methods to account for heterogeneous variances in genetic prediction models is required, to allow unbiased selection.

Herd-year-season of calving, parity and age at calving are significant causes of variation in milk, fat and protein yield of South African Holstein cattle. Differential effects of these effects, between the two production systems, may be the cause of heterogeneous variances. These environmental factors need to be included in models for genetic evaluation of these traits. Exclusion of these factors may result in reduced accuracy of the genetic prediction models, leading to a decrease in rate of genetic gain.

Heritability estimates for milk, fat and protein yield obtained in the current study indicate the potential for significant response to selection on these traits in the South African Holstein cattle population. Larger heritability estimates in the low input production system suggest that animals are genetically diverse, thus creating a large scope for genetic improvement through selection.

High and positive genetic correlations for milk, fat and protein yields indicate that selection for either of the traits will result in a correlated response for the other two traits. The high degree of association among milk production traits of South African Holstein cattle provides a favourable basis for multiple trait genetic evaluation of these traits and their inclusion in the breeding objective.

The positive genetic trends for milk, fat and protein yield obtained in the high input production system indicate that there has been a significant improvement in these traits during the time period considered. However, a downward genetic trend with high heritability estimates observed in the low input production system suggests that genetically inferior animals were used for breeding. This highlights the need for developing a sound breeding program for this production system. The high heritability estimates in the low input production system indicate that, given enough investment, substantial genetic improvement of Holstein cattle in the small-holder and emerging farms can be achieved through selection.

Chapter 7 : REFERENCES and APPENDICES

ALBUQUERQUE, L.G., KEOWN, J.F. & VAN VLECK, L.D. 1996. Genetic parameters of milk, fat and protein yields in the first three lactations, using an animal model and restricted maximum likelihood. *Brazilian Journal of Genetics*, 19: 79-86.

ANDERSON, R. 1985. Mammary Gland. In: Larson B.L. (Ed.). Lactation, Ames, IA: Iowa State University Press, 3-38.

BANGA, C.B., NESER, F.W.C., VAN DER WESTHUIZEN, J. & GARRICK, D.J. 2009. Economic values for dairy production traits under different milk payment systems in South Africa. *South African Journal of Animal Science*, 39 (1): 112-115.

BANGA, C.B., NESER, F.W.C. & GARRICK, D.J., 2014. Breeding objectives for Holstein cattle in South Africa. *South African Journal of Animal Science.* 44, 199-214.

BOHLOULI, M., ALIJANI, S. & VARPOSHTI, R.M. 2015. Genetic relationships among linear type traits and milk production traits of Holstein dairy cattle. *Journal of Animal Science*, 15 (4): 903-917.

BOHMANOVA, J., MISZTAL, I. AND COLE, J.B., 2007. Temperature-humidity indices as indicators of milk production losses due to heat stress. *Journal of Dairy Science*, *90*(4), 1947-1956.

BOLDMAN, K. G. 1989. Heterogeneity of variances by herd production level and its effect on dairy cow and sire evaluation. *Ph.D. Dissertation. (Microfilm No. DEW8920113) Iowa State University, Ames.*

BOLDMAN, K.G. AND FREEMAN, A.E., 1990. Adjustment for heterogeneous variances by herd production level in dairy cow and sire evaluation. *Journal of Dairy Science*, 74, 503-512.

BROTHERSTONE, S. & HILL, W.G., 1986. Heterogeneity of variance amongst herds for milk production. Anim. Prod. 42, 297-303 herd production level in dairy cow and sire evaluation. *Journal of Dairy Science* ,74, 503-512.

CARNEIRO, J.J.M., ASSIS, G.L.M., EUCLYDES, R.F., LOPES, P.S., 2007. Estimação de componentes de variância utilizando-se inferência Bayesiana e freqüentista emdados simulados sob heterogeneidade de variâncias. *Revised By Zootechnology.* 36, 1539–1548 *(translated from Portuguese)*

CERÓN-MUÑOZ M.F, TONHATI H, COSTA C.N, ROJAS-SARMIENTOAD D, SORLATE PORTILLA C., 2004. Variance heterogeneity for milk yield in Brazilian and Colombian Holstein herds. *Journal of Animal Science*, 21 (6): 800-816.

CHINOGARAMOMBE, G.N.C., MUCHENJE, V., MAPIYE, C., NDLOVU, T., CHIMONYO, M AND MUSEMWA, L., 2008. Challenges for improving smallholder dairy production in the semi-arid areas of Zimbabwe. *Livestock Research for Rural Development. Crops*, 7(1): 0-3.

COSTA, C.N., 1999. An investigation into heterogeneity of variance for milk and fat yields of Holstein cows in Brazilian herd environments. *Genetics and Molecular Biology* 22,375–381.

DODENHOFF, J., SWALVE, H.H., 1998. Heterogeneity of variances across regions of northern Germany and adjustment in genetic evaluation*.* *Livestock Production Science* 53,225–236

DUBE, B. 2006. Genetic Parameters and Trends of Somatic Cell Score and Udder Type Traits in South African Holstein and Jersey Cows. MSc Dissertation, University of Fort Hare, Eastern Cape, South Africa.

ERFANI-ASL, Z., HASHEMI, A. & FARHADIAN, M. 2015. Estimates of Repeatability and Heritability of Productive Trait in Holstein Dairy Cattle. *Iranian Journal of Applied Animal Science*, 5 (4): 827-832.

ESSL, A., 1998. Longevity in dairy cattle breeding: a review. *Livestock Production Science*, *57*(1), pp.79-89.

EVERETT, R.W., KEOWN, J.F. AND TAYLOR, J.F. (1982). The problem of heterogeneous within herd error variances when identifying elite cows. *Journal of Dairy Science* 65(4)*.*13-27

FALCONER, D.S. 1989 *Introduction to Quantitative Genetics*, 3rd ed. Longman, London and New York.

FAO, 2011. Dairy Development in Kenya. Rome, Italy.

GARRICK, D.J. & VAN VLECK, L.D. 1987. Aspects of selection for performance in several environments with heterogeneous variance. *Journal of Dairy Science 65, 409-421*

FLEMING, A., ABDALLA, E.A., MALTECCA, C. AND BAES, C.F., 2018. Invited review: Reproductive and genomic technologies to optimize breeding strategies for genetic progress in dairy cattle. *Archiv fuer Tierzucht*, *61*(1), p.43.

GILMOUR, A.R., CULLIS, B.R., WELHAM, S.J. & THOMPSON, R. 2001. ASREML. Reference Manual. Program user manual, NSW Agriculture, Orange Agricultural Institute, NSW, Australia.

GILMOUR, A. R., B. J. GOGEL, B. R. CULLIS, AND R. THOMPSON. 2009. ASReml User Guide Release 3.0. VSN International Ltd., Hemel Hempstead, UK.

GUZZO, N., SARTORI, C., MANTOVANI, R., 2018. Heterogeneity of variance for milk, fat and protein yield in small cattle populations: The Rendena breed as a case study. *Livestock Science* 213, 54–60

HALLOWELL, G.J., VAN DER WESTHUIZEN, J. & VAN WYK, J.B. 1998. Variance component and heritability estimates for first and second lactation milk traits in the South African Ayrshire breed. *South African Journal of Animal Sciences,* 20 (1): 46-49.

HAZEL, L.N. 1943. The genetic basis for constructing selection indexes. *Genetics*, 28: 476-490.

HENDERSON, CR. 1984. Application of Linear Models in Animal Breeding. University of Guelph, Ontario, Canada.

HEMME, T AND OTTE, J., (2010). Status and Prospects for Smallholder Milk Production A Global Perspective. FAO, Rome, Italy.

HILL, W.G., 1984. On selection among groups with heterogeneous variance. *Animal Production* 39, 473–477.

KABUGA, J.D. AND AGYEMANG, G.K. 1984.Performance of Canadian Holstein-Friesian cattle in the humid forest zone of Ghana. 1. Milk production. *Tropical of Animal Health and Production*., 16(2): 85-94.

KARIUKIA C.M, VAN ARENDONKC, J.A.M, KAHID A.K AND KOMENA H. Deterministic simulations to determine the impacts of economic and noneconomic breeding objectives on sustainable intensification of developing smallholder dairy farms. *Livestock Science* 226, 7–12.

KEKANA, T F., 2017. Genetic parameter estimates among milk production traits for the first three lactations in South African Guernsey cattle. MSc Dissertation, Tshwane University of Technology, Gauteng, South Africa.

LACTO DATA. 2011. Statistics a milk SA publication compiled by the Milk Producers Organisation, 14(2).

LACTO DATA. 2016. Statistics a milk SA publication compiled by the Milk Producers Organisation, 19(1).

LACTO DATA. 2017. Statistics a milk SA publication compiled by the Milk Producers Organisation, 20(1).

LINO-LOURENÇO, D.A., LOPES DE OLIVEIRA, C.A., MARTINS, E.N., PAULA LEITE, M.C.,MAIAAND, F.C.M., SANTOS, A.I., 2012. Heterogeneous genetic (co)variances in simulated closed herds under selection. *Maringá* 34, 83–90.

LIU, S., TAN, H., YANG, L. & YI, J. 2014. Genetic parameter estimates for selected type traits and milk production traits of Holstein cattle in southern China. *Turkish Journal of Veterinary and Animal Sciences,* 38: 552-556.

LOGAR, B. AND JERETINA, J., 2015. Web advisory tools to support dairy production in Slovenian herds. In: Performance recording in the genotyped world,

KOWALSKI, Z., PETRENY, N., BURKE, M., BUCEK, P.,JOURNAUX, L., COFFEY, M., HUNLUN, C. AND RADZIO, D. (editors),ICAR Technical Series 2015, No. 19, pp. 73–78. Proceedings of the ICAR Technical Meeting held in Krakow, Poland, 10–12 June, 2015.

LUSH, J.L. 1937. Animal Breeding Plans. Collegiate Press, Inc., Ames.

M'HAMDI, N., BOUALLEGUE, M., FROUJA, S., RESSAISSI, Y., BRAR, S.K. & HAMOUDA, M.B. 2012. Effects of Environmental Factors on Milk Yield, Lactation Length and Dry Period in Tunisian Holstein Cows and kept on farms under the Turkish-ANAFI project. *Italian Journal of Animal Science*, 2: 141-150.

MACKLE, T.R., BRYANT, A.M., PETCH, S.F., HOOPER, R.J. AND AULDIST, M.J., 1999. Variation in the composition of milk protein from pasture-fed dairy cows in late lactation and the effect of grain and silage supplementation. *New Zealand Journal of Agricultural Research*, *42*(2), pp.147-154.

MADALENA, F.E., 2008. How sustainable are the breeding programs of the global mainstream dairy breeds? – The Latin-American situation. Livestock Research Rural Development. 20 (2).

MAGOTHE, T.M., ILATSIA, E.D., WASIKE, C.B., MIGOSE, S.A. & KAHI, A.K., 2006. Genetic evaluation of milk yield of *Bos taurus* dairy breeds in Kenya. In. Proceedings of the 10th KARI scientific conference, Nairobi, Kenya (in press).

MAKGAHLELA, M.L. 2006. Genetic analysis of female fertility traits and their relationship with yield traits in South African Holstein. Msc Dissertation, University of Limpopo, Limpopo, South Africa.

MAKGAHLELA, M.L., BANGA, C.B., NORRIS, D., DZAMA, K. & N'GAMBI, J.W., 2006. Genetic correlation of female fertility traits and their relationships with yield traits in South African Holstein cattle. *South African Journal of Animal Science 37(3), 180–188*.

MAPEKULA, M., MAPIYE, C AND CHIMONYO, M. (2011). Changes in metabolites concentration in Nguni and crossbred calves on natural pasture. Asian-Australian Journal of Animal Science, 24(11): 1569-1576.

MISSANGJO, E., IMBAYARWO-CHIKOSI, V. & HALIMANI, T. 2013. Estimation of Genetic and Phenotypic Parameters for production Traits and Somatic Cell Count for Jersey Dairy Cattle in Zimbabwe. *International Scholarly Research Notices: Veterinary Science*, 10: 1155.

MOLOI, M.J. 2010. A comparison of socioeconomic characteristics that determine the farm income of emerging livestock and horticultural farmers in South Africa. Doctoral dissertation. University of Limpopo. Limpopo, South Africa.

MOSI, R.O. (1984) .The use of milk records in cow evaluation and Dairy cattle improvement in Kenya. Ph.D. Thesis, University of Wales.

MOSTERT, B.E., THERON, H.E. & KANFER, F.H.J. 2001. The effect of calving season and age at calving on production traits of South African dairy cattle. *South African Journal of Animal Science*, 31 (3): 205-214.

MOSTERT, B.E. AND THERON, H.E. AND KANFER, F.H.J. AND VAN MARLE-KOSTER E, 2006. Test-day models for South African dairy cattle for participation in international evaluations. *South African Journal of Animal Science*, 36, 58-70.

MOSTERT, B.E. 2007. The suitability of test-day models for genetic evaluation models for genetic evaluation of dairy cattle in South Africa. PhD Thesis, University of Pretoria, South Africa.

MUASYA, T.K., ILTSIA, E.D., MAGOTE, T.M., KAHI, A.K., 2007. Heterogeneity of variance and its implications on dairy cattle breeding. *South African Journal of Animal Science 37, 170–175.*

POWELL, R.L., NORMAN, H.D. AND WEINLAND, B.T. (1983). Cow evaluationat different milk yield of herds. *Journal of Dairy Science* 66: 148-154.

NATIONAL DAIRY ANIMAL IMPROVEMENT SCHEME 2011. Annual Report 2011 Volume 31. Agricultural Research Council, South Africa.

NAYA, H., URIOSTE, J.I. & FRANCO, J., 2002. Identification of production environments and presence of G x E interactions in Uruguay using Holstein herds records. In Proc. 7th World Congress on Genetics Applied to Livestock Production, August 19-23, 2002, Montpellier, France.

NIKOLAOU, M.KOMINAKIS, A.P.ROGDAKIS, E.ZAMPITIS, S, 2004. Effect of mean and variance heterogeneity on genetic evaluations of Lesbos dairy sheep. Livestock Production Science 88:107- 115.

NILFOROOSHAN, M.A. 2010. Contemporary grouping in mixed-size dairy herds experiencing four seasons. Journal of Veterinary Animal Science, 34(2): 129-135.

NJUBI D M, WAKHUNGU J AND BADAMANA M S., 2009**.** Milk yield prediction in Kenyan Holstein-Friesian cattle using computer neural networks system. *Livestock Research for Rural Development. Volume 21(46).*

NTSHEPHE, L., (2011). Marketing information needs of smallholder livestock farmers in the Morele area. Master's Thesis, University of South Africa, Pretoria, South Africa

OJANGO J M K AND POLLOTT G E., 2001. Genetics of milk yield and fertility traits in Holstein-Friesian cattle on large-scale Kenyan farms. Journal of Animal Science 79: 1742-1750.

OKENO, T.O., KOSGEY, I.S., KAHI, A.K., 2010. Economic evaluation of breeding strategies for improvement of dairy cattle in Kenya. Trop. Anim. Health Prod. 42, 1081–1086.

OLUKOYE, G.A. & MOSI, R.O., 2002. Non-genetic causes of heterogeneity of variance in milk yield among Holstein-Friesian herds in Kenya. The Kenya Veterinarian 25, 18-23.

OOSTING, S.J., UDO, H.M.J., VIETS, T.C., 2014. Development of livestock production in the tropics: farm and farmers' perspectives. Animal 8, 1238–1248.

PETROVIĆ, D.M., SKALICKI, Z., PETROVIĆ, M. M., BOGDANOVIĆ, V. 2009. The effect of systematic factors on milk yield in Simmental cows over complete lactations. Journal of Biotechnology in Animal Husbandry, 25: 61-71.

Přibyl, Josef & Pribylova, J. (2001). Variability of milk production within the contemporary groups in prediction of breeding value. Czech Journal of Animal Science. 46. 514-522.

RAFFRENATO, E., BLAKE, R.W., OLTENACU, P.A., CARVALHEIRA, J. & LICITRA, G., 2003. Genotype by environment interaction for yield and somatic cell score. *Journal of Dairy Science* 86, 2470–2479.

REGE J E O AND MOSI R O., 1989. Analysis of the Kenyan Friesian breed from 1968 to 1984: genetic and environmental trends and related parameters of milk production. Bulletin of Animal Health and Production in Africa 37:267.

RICA, C., VARGAS, B., VAN ARENDONK, J.A.M., 2004.Genetic comparison of breeding schemes based on semen importation and local breeding schemes: framework and application to Costa Rica. J. Dairy Sci. 87, 1496–1505.

RÖNNEGÅRD, L., FELLEKI, M., FIKSE, W.F., MULDER, H.A., STRANDBERG, E., 2013. Variance component and breeding value estimation for genetic heterogeneity of residual variance in Swedish Holstein dairy cattle. *Journal of Dairy Science* 96, 2627–2636.

SAS. 2013. Statistical Analysis Systems. SAS User Guide: Release 9.3. Statistical Analysis System Institute, Inc., Cary, North Carolina, USA.

SCHROOTEN, C., M. C. A. M. BINK, AND H. BOVENHUIS. 2004. Whole genome scan to detect chromosomal regions affecting multiple traits in dairy cattle. J. Dairy Sci. 87: 3550- 3560.

SENYOLO, G. M., CHAMINUKA, P., MAKHURA, M. N., & BELETE, A. 2009. Patterns of access and utilization of output markets by emerging farmers in South Africa: Factor analysis approach. African Journal of Agricultural Research, 4 (3): 208-214.

SOUTH AFRICAN YEARBOOK. 2009/10. Department of Agriculture, Forestry and Fisheries, South Africa.

SOUTH AFRICAN YEARBOOK. 2015/16. Department of Agriculture, Forestry and Fisheries, South Africa.

STATS S.A.2018. Mid-year population estimates – 2018. Statistical Release P0302. 1 July. Pretoria: Statistics South Africa.

STOTZ, D., 1983. Production techniques and economics of smallholder production systems in Kenya. In: Farm Management Handbook of Kenya, Vol. IV, Nairobi, Kenya.

SYRSTAD, O. (1965) Studies on dairy herd records. 2. Effect of age and season of calving. *Acta. Agric. Sand.,* 15: 31-64.

TANYANYIWA, F.K. 2016. An assessment of entrepreneurial attributes determining the potential of smallholder dairy farmers progressing to commercial farming. Msc Dissertation, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

TESFA, K.N., VAN WYK J.B. AND NESER, F.W.C. 2004. Genetic parameter estimates in South Africa Holstein cattle. South African Journal of Animal Science, 34(2): 92-94.

THINDISA, L. M. V., (2014). Participation by smallholder farming entrepreneurs in agro-processing activities in South Africa. (Doctoral dissertation). University of the Witwatersrand, South Africa.

The Holstein breed, http://www.holsteinusa.com/holstein_breed/breedhistory.html

TIAPD, 2016. Report of a study on assessing the cost of production structures in dairy systems in Kenya. Nairobi, Kenya.

TORSHIZ, M. E. 2016. Effects of season and age at first calving on genetic and phenotypic characteristics of lactation curve parameters in Holstein cows. *Journal of Animal Science and Technology*, 58(8): 1-14.

VAN ALFEN, K.N. 2014. Encyclopedia of Agriculture and Food Systems. University of California, Davis, CA, USA. ISBN: 978-0-444-52512-3.

VINSON, W.E., 1987. Potential bias in genetic evaluations from differences in variation within herds. *Journal of Dairy Science* 70, 2450–2455.

VINSON, W.E., 1987. Potential bias in genetic evaluations from difference in variation within herds. J. Dairy Sci. 70, 2450-2455.

WEIGEL, K.A. & REKAYA, R., 2000. A multiple-trait herd cluster model for international dairy sire evaluation. *Journal of Dairy Science* 83, 815–821.

WILSON, R.T., 2009. Fit for purpose – the right animal in the right place. Trop. Anim. Health Prod. 41, 1081–1090.

WINKELMAN, A., SCHAEFFER, L.R., 1988. Effect of heterogeneity of variance on dairy sire evaluation*. Journal of Dairy Science* 71, 3033–3039.

WRAY, N. &VISSCHER, P. 2008. Estimating trait heritability. *Nature Education* 1(1):29

ZAABZA, H.B., GARA, A.B, HAMMAMI, H., FERCHICHI, M.A & REKIK, B. 2016. Estimation of variance components of milk, fat, and protein yields of Tunisian Holstein dairy cattle using Bayesian and REML methods. Archives Animal Breeding Journal, 59: 243-248.

APPENDICES

Appendix A: Milk

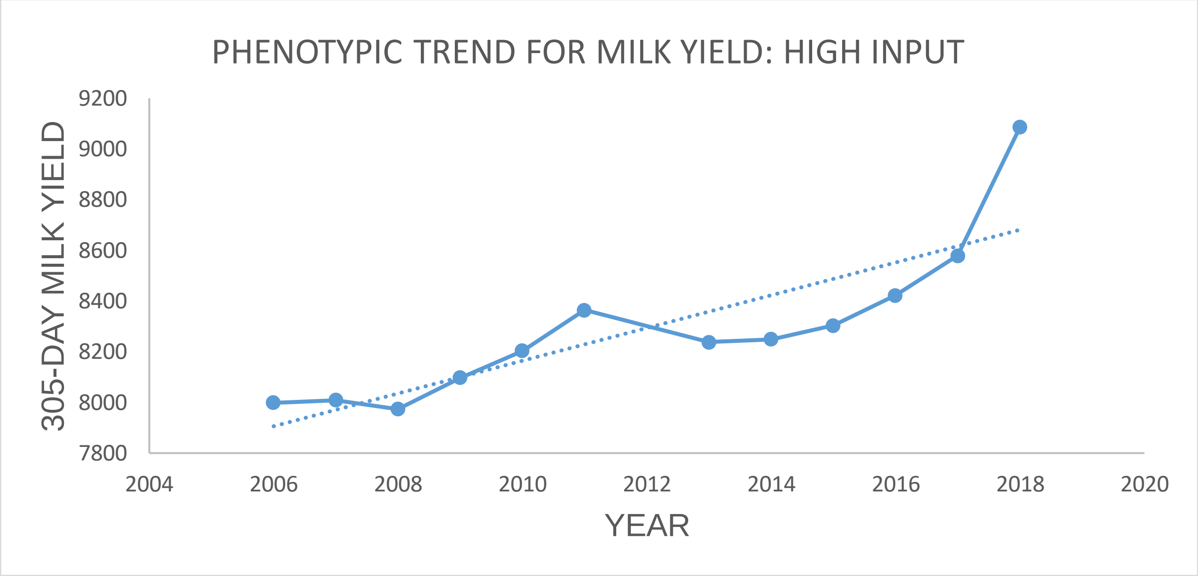

Figure 7.1: Phenotypic trends for milk yield in the high input production system

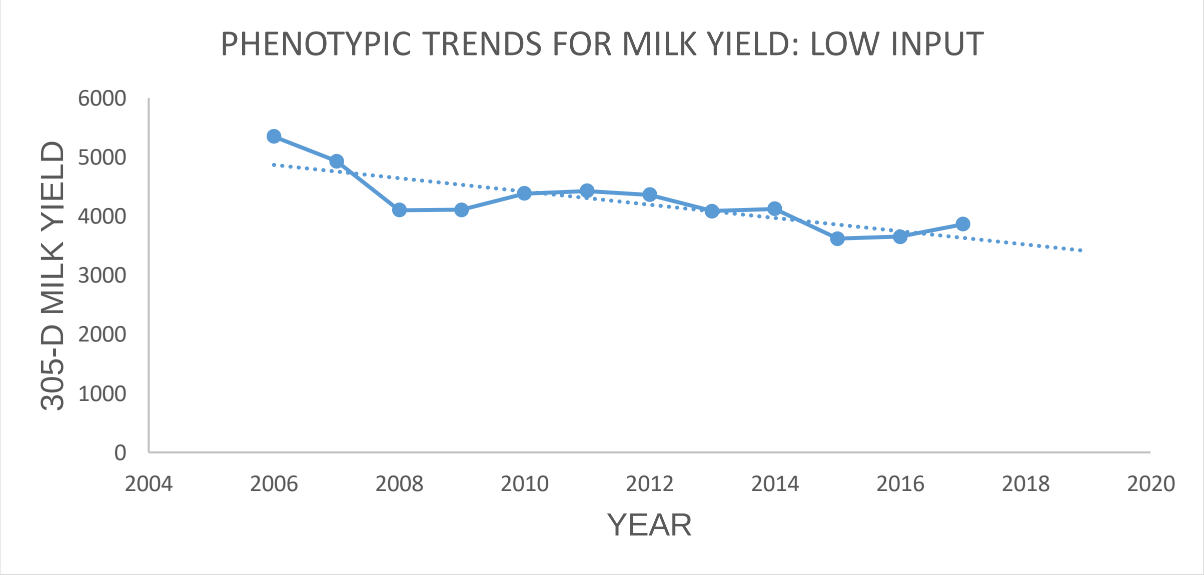

Figure 7.2: Phenotypic trends for milk yield in the low input production system

Appendix B: Fat

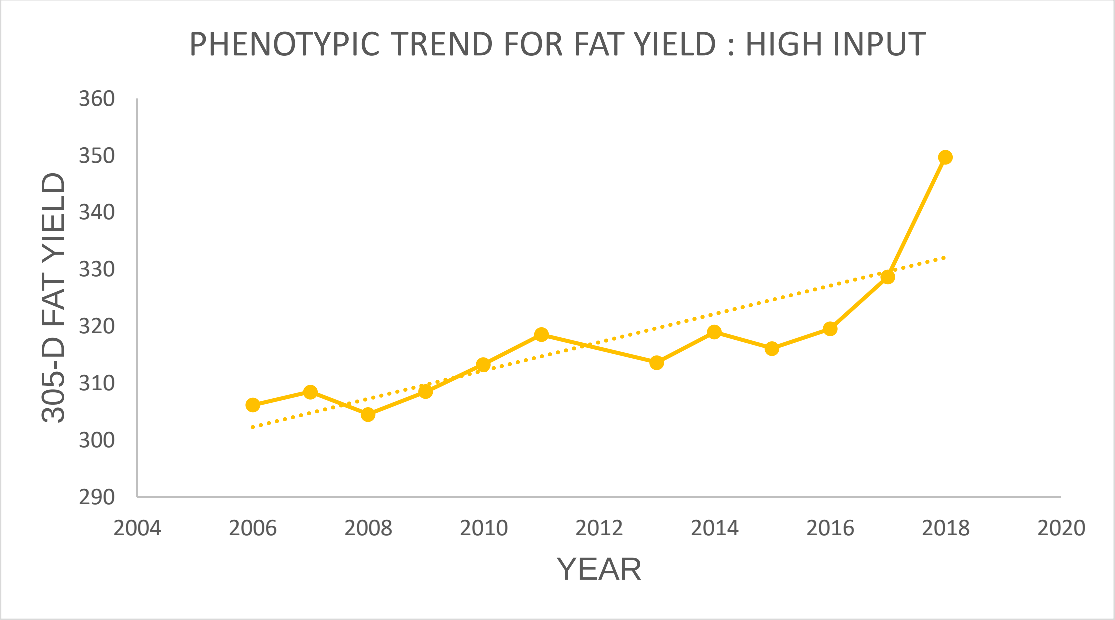

Figure 7.3: Phenotypic trends for fat yield in the high input production system.

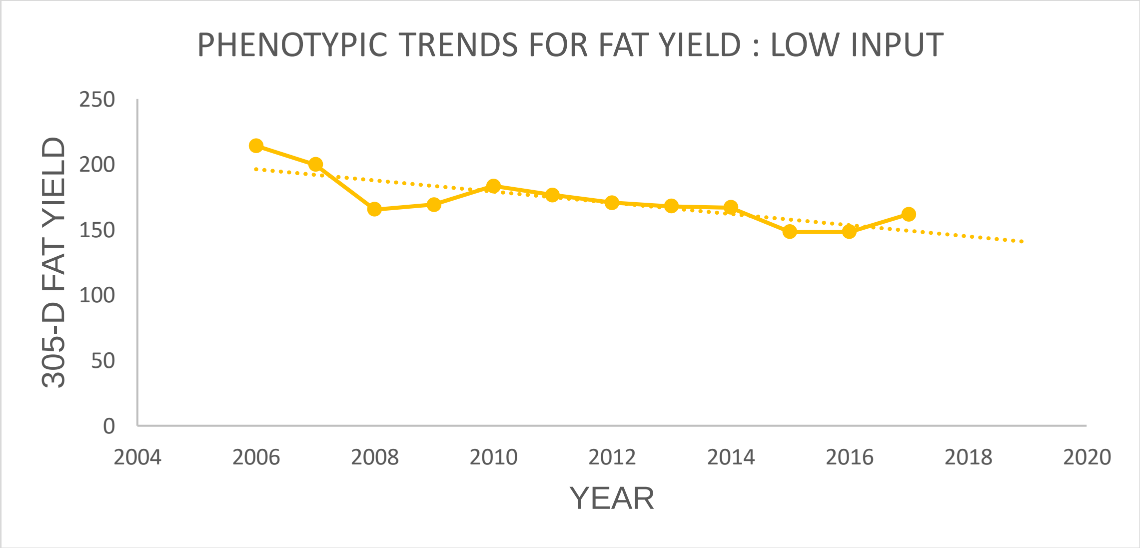

Figure 7.4: Phenotypic trends for fat yield in the high low production system.

Appendix C: PROTEIN

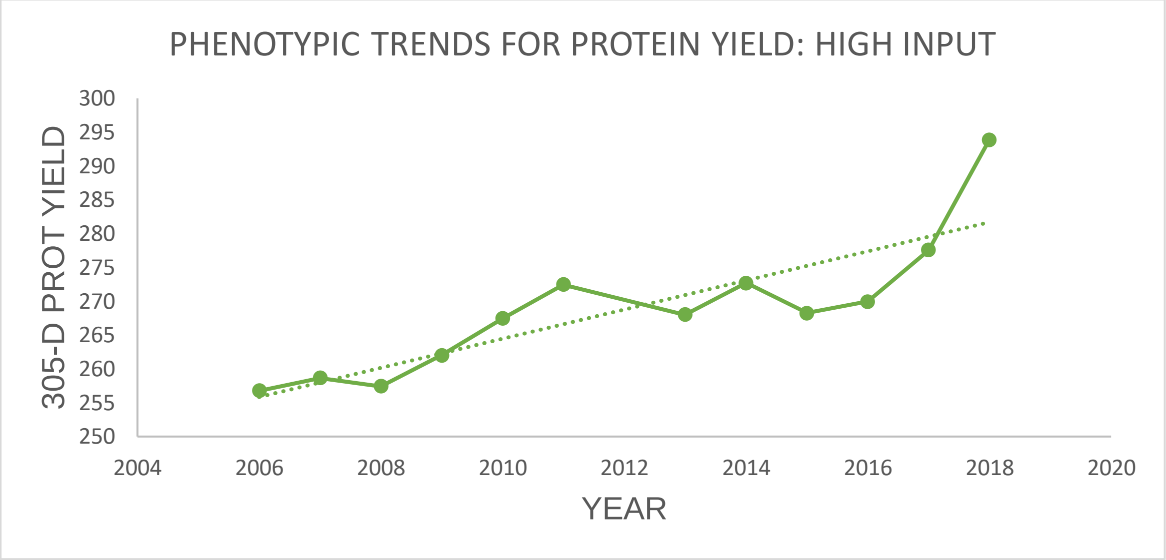

Figure 7.5: Phenotypic trends for protein yield in the high input production system.

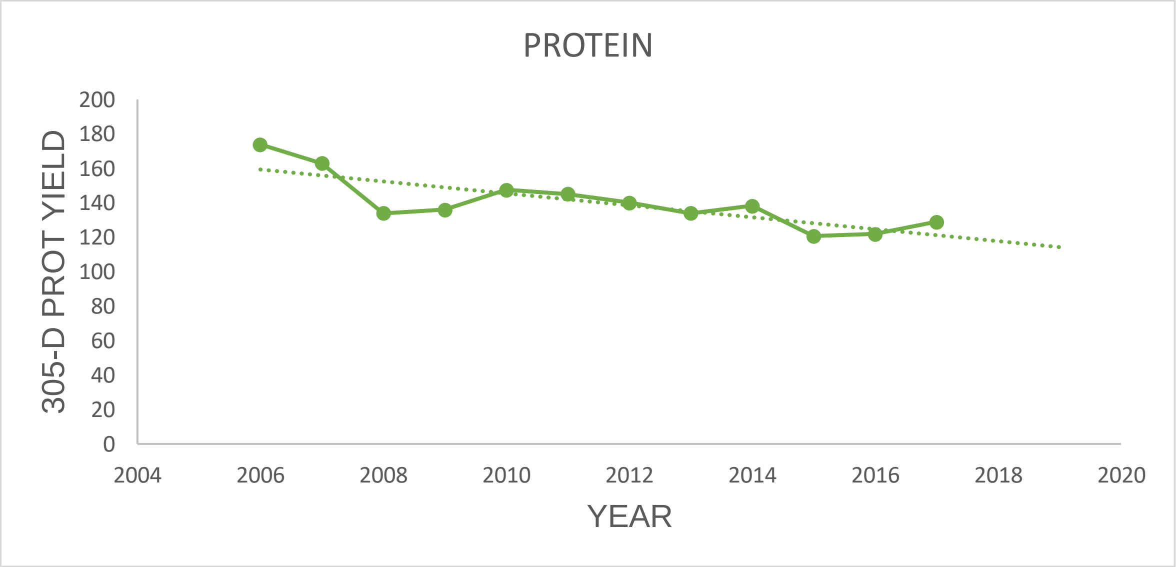

Figure 7.6: Phenotypic trends for protein yield in the low input production system.