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Effect of the production environment on the production efficiency of Bonsmara cows in South Africa

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PREFACE

The work described in this dissertation was carried out at the Department of Animal and Wildlife Sciences, University of Pretoria, Pretoria, from Jan 2010 to December 2011, under the supervision of Professor Edward C. Webb

I declare that the dissertation, which I hereby submit for the degree MSc(Agric) Animal Science: Production Management at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date: 2012/09/25

Abstract

The production environment is known to have a large influence on extensively managed beef cows. A better understanding of the relationship between the beef cow and her environment should be useful in the pursuit of improving beef cow efficiency. The influence of the production environment on the efficiency of extensively managed Bonsmara cows was investigated through a series of research objectives. It was found that VEGMAP's bioregion classification system can be used to describe the South African beef production regions. The environmental characteristics with the potential to influence beef cow efficiency were identified as temperature, rainfall, cation exchange capacity, soil pH, soil organic carbon, soil P and grazing capacity. A dataset was created that contains the historical cow production records for every Bonsmara breeder. GIS tools were then used to link the cow production records with the production region in which the farm is located, as well as the environmental characteristics for that specific location. The combined dataset was then statistically analysed to investigate the research objectives. The influence of the geographic location, production region and breeder on Bonsmara production traits was investigated by cluster analysis and ANOVA. Results from ANOVA indicate that production region has a statistically significant ($p < 0.05$) influence on production traits. The influence of the breeders on the same production traits was, however, statistically much larger ($p < 0.0001$) than production region. Bonsmara production traits are therefore influenced to a greater extent by the breeders rather than production environment. Stepwise regression analysis was used to determine the influence of the combined environment on production traits. The combined environment has a statistically significant ($p < 0.0001$) influence on all the production traits. The results indicate that the extent of the influence of the environment on production change through the growth curve. The environment's influence was the greatest at weaning (9%) and yearling age (10%). Bonsmara weaning and yearling weights therefore show the largest potential for manipulation through management. The influence of individual environmental characteristics on all the Bonsmara cow production traits was then investigated by the same stepwise regression analysis. Most of the environmental characteristics were found to have a statistically significant ($p < 0.0001$) influence on the production traits. Rainfall and temperature had the largest influence on Bonsmara production traits. The negative influence of rainfall was attributed to the influence of rainfall on the quality of the grazing. The influence of temperature on production traits was small. The small negative influence of temperature could indicate that Bonsmara cows are well adapted to the main South African beef production regions. Finally, the relationship between Bonsmara cow size and reproduction was investigated by linear regression analysis. Results indicate that larger Bonsmara cows are to some extent more reproductive than smaller cows. The study confirmed that production environment influences beef cow efficiency. Bonsmara breeders however have a much larger influence on the efficiency of their cows through the implementation of management practices and breeding objectives.

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Abbreviations

12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
AFC	Age at first calving
AFC_E	Environmental component of age at first calving
AGIS	Southern African Agricultural Geo-referenced Information System
ARC-API	Agricultural Research Council-Animal Production Institute
ARC-ISCW	Agricultural Research Council Institute for Soil Climate and Water
BLUP	Best linear unbiased predictions
BW_E	Environmental component of birth weight
CEC	Cation exchange capacity
DAFF	Department of Agriculture, Fisheries and Forestry
DoA	Department of Agriculture
E	Environment
EBV	Estimated Breeding Value
FSH	Follicle stimulating hormone
G	Genotype
G x E	Genotype environmental interaction
GC	Grazing capacity
GIS	Geographic information system
h^2	Heritability
i	Selection intensity
ICP	Inter-calving period
ICP_E	Environmental component of inter-calving period
ICTP	International Commission for Thermal Physiology
L	Generation interval
LH	Luteinising hormone
LSM	Least square means
LTHA	Long-term heat adaptation
MW	Mature weight (weight at 4 years)
MW_E	Environmental component of mature weight
NEFA	Non-esterified fatty acids
NDVI	Normalised difference vegetation index
P	Phenotype
pH	Soil pH
PPI	Postpartum anoestrus
R	Selection
R	Rainfall
RI	Reproduction index
SANBRIS	South African National Beef Recording and Improvement Scheme
SAWS	South African Weather Service
SOC	Soil organic carbon
STHA	Short-term heat acclimation
T	Temperature
THI	Temperature humidity index
WW_E	Environmental component of wean weight

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“*Cattle breeding is a relatively simple endeavour. The only difficult part is to keep it simple*”.
Tom Lasater

A humble start— my first stud calf

CHAPTER 1
INTRODUCTION

1.1. MOTIVATION

Livestock products account for more than 40% of the total value of South Africa's agricultural output (DAFF, 2003). Only 15% of South Africa's land area is suitable for arable farming and 40% of the remaining 85% surface area receives less than 375 mm rain per annum (Tainton, 1999). The South African National Strategic Plan for Agriculture consequently points out that room for horizontal expansion of agriculture is restricted due to environmental constraints, and that increased agricultural production can only be achieved by improving the efficiency of production (DAFF, 2003). There is, therefore, a need to improve the efficiency of livestock production in South Africa. The long term improvement of the efficiency of animal production can only be achieved through the identification and selection of genetically superior animals for breeding purposes (Lush, 1994; Scholtz *et al.*, 2010). The selection of genetically superior animals can be done on the basis of a combination of pedigree information, appearance and performance-recorded information and breeding values (Lush, 1994; Scholtz *et al*., 2010). It has also been suggested that beef cow efficiency can be improved by tailoring cow size to environment and improving adaptive ability (Bonsma, 1983; Kattnig *et al*., 1993). This suggestion is due to the important influence that cow size has on the way that the cow responds to the environmental stressors (Arango & Van Fleck, 2002) and her ability to adapt to that environment (Bonsma, 1983). Cattle that are adapted to their environment are able to tolerant adverse environmental conditions and are able to maintain reproductive efficiency (Prayaga & Henshall, 2005).

The importance of the adaptive ability of beef cattle was highlighted at the at the 2005 Beef Improvement Federation (BIF) symposium. Hohenboken *et al*. (2005) reported certain recommendations that were considered necessary to improve genetic gains for adaptation in beef cattle in the U.S.A. Two recommendations were that the major beef cattle production environments should be identified and their nutritional, physical, climatic, management and economic characteristics characterised. Hohenboken *et al*. (2005) also stressed that the major physical, biotic, social and management stressors for each environment have to be defined.

The influence of production region on cattle production has been investigated by a number of authors both locally (Bonsma, 1983; Ronchietto, 1993; Botsime, 2005; Nqeno, 2008) and internationally (Cundiff *et al*., 1966., Dooley *et al*., 1982; Leighton *et al*., 1982; Burfening *et al*., 1987). It is suggested that the natural variation in size of the same species of wild animals occurring in different environments is an indication that nature defines the "right" genetic material for efficiency in different ways in different environments (Johnson *et al*., 2010). The existence of optimal cow size for specific environments has been investigated by numerous authors (Dickerson, 1970; Morris & Wilton, 1976; Anderson, 1978; Fitzhugh, 1978; Bonsma, 1983; Buttram & Willham, 1989; Brown, *et al*., 1989; Johnson, *et al*., 1990; Arango & Van Fleck, 2002; Johnson *et al*., 2010; Echols, 2011). From the literature it is evident that the production environment has a strong influence on beef cow efficiency, although there is little consensus regarding the existence of optimal mature cow size for specific production environments. It can therefore safely be assumed that the efficiency of beef cows is influenced by a combination of size, adaptive ability and production environment. An investigation into the relationship between these characteristics should be useful for improving beef cow efficiency and overall beef production in South Africa.

The Bonsmara is the dominant South African beef cattle breed with more than 100 000 registered animals (Scholtz *et al*., 2010). Prof. J.C. Bonsma played a leading role in the development of the Bonsmara breed and the "Breeding for functional efficiency" concept employed by the Bonsmara Cattle Breeders Society. The Bonsmara was based on a 5/8 Afrikaner and 3/8 Exotic (Shorthorn/Hereford) breeding admixture and considerable emphasis was placed on selection for adaptive ability (Bonsma, 1983). Bonsmara breeding stock must be functionally efficient and all Bonsmara cattle must be screened for functional efficiency by herd inspectors before they can be registered as stud animals. The Bonsmara functional efficiency concept is based on the assumption that selection for phenotypic traits that has an influence on the animal's ability to adapt to the environment will improve the animal's ability to express its reproductive and productive potential (Bonsma, 1983). Bonsmara breeders commonly assume that specific types or sizes of cattle are better adapted to specific production regions. This assumption originated from Prof. J.C. Bonsma who argued that cows that are adapted and are of optimal size for the environment in which they occur will be able to produce and reproduce to their full genetic potential. However, these concepts have not been proven conclusively and remain controversial.

The Bonsmara breed, such as all pedigree breeds, has a hierarchical breeding structure. This structure is shown in Figure 1.1. The hierarchy consists of three levels. The top or breeder herds known as "elite breeders" furnish breeding material to each other and to middle-order breeders. The middle-order breeders in turn sell breeding material among themselves and to the lower group of breeders, but seldom sell animals back to the elite breeders. The lower group, called "multiplier breeders", in turn supplies genetic material to other multipliers as well as commercial breeders (Lush, 1994; Hunlun, 2009).

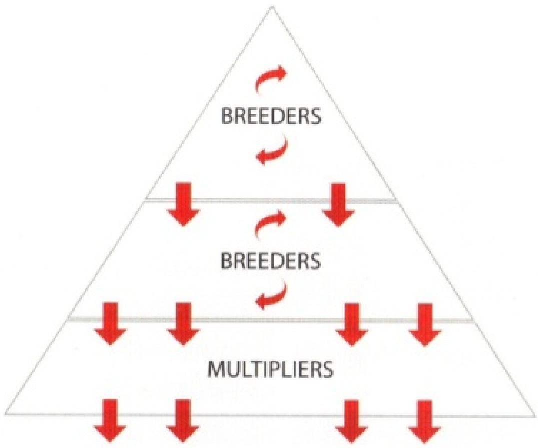

Figure 1.1 Bonsmara pedigree breed hierarchy (Hunlun, 2009)

Hunlun (2009) analysed the breed structure of the Bonsmara and found that there are 16 Bonsmara breeders that each contribute more than 1% of the genetic make-up of the South African Bonsmara cattle population. The combined genetic contribution of the 16 elite breeders makes up 30.4% of the genetic composition of the entire Bonsmara population. The top breeder contributes 5.37% to the genetic composition of the breed while the next herd contributes 3.07% to the genetic composition. Given the substantial influence that the 16 elite breeders have on the genetic make-up of the Bonsmara population it is safe to assume that the breeding objectives as well as type and size of Bonsmara of these 16 breeders will have a large influence on the Bonsmara "types" kept by multiplier and commercial breeders.

The localities of the 15 elite breeders (one breeder has since left farming) are shown in Figure 1.2. From the distribution map it is evident that the elite breeders are evenly distributed throughout the main South African beef-production regions. The distribution of these breeders suggests that the elite Bonsmara breeders do not favour any specific area in South Africa. If there are, as is believed, optimum-sized animals for each production region, the dominating influence of the elite breeders could have a negative influence on the Bonsmara population's production efficiency. It is reasonable to accept that the genetic material of the elite breeders would be distributed between different production environments and if there are an optimal cow size for each environment the relocated animals, and their progeny, would not necessarily be adapted to the new different production environment. The identification of production region and characterisation of optimal mature cow size for each production region would be a valuable tool for breeders in setting breeding goals and would act as a guide from which area to purchase breeding animals.

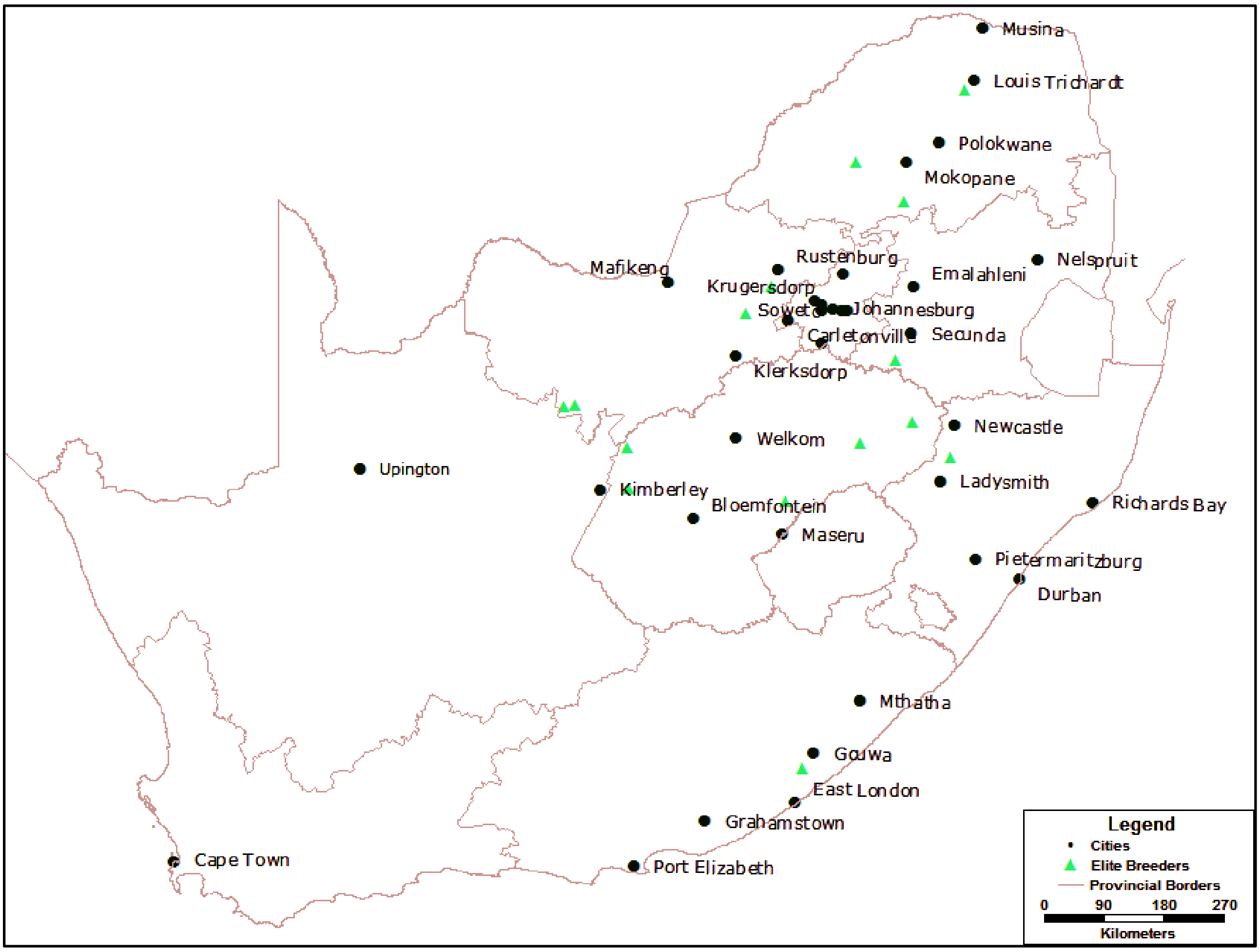

Figure 1.2 Locations of elite Bonsmara breeders in South Africa

Another consequence of the breeding structure of the Bonsmara breed is that the breeding objectives of the elite Bonsmara breeders identified by Hunlun (2009) will determine the direction of genetic change for the entire Bonsmara population. The breeding objectives regarded as most important by Bonsmara breeders are reproduction, maternal environment and growth (J. van der Westhuizen. Personal Communication. S.A Studbook. 2011). Genetic trends for growth and maternal traits in the Bonsmara breed are shown in Figure 1.3 while the genetic trends for reproduction traits are indicated in Figure 1.4 (ARC-API). Genetic trends are shown from 1990, the year that is used as the base year for the Bonsmara breeding value predictions (EBVs). The graph shown in Figure 1.3 indicates that Bonsmara breeders have managed to increase the growth efficiency of the breed by greatly improving the wean direct and maternal components as well as 12- and 18-month weights without appreciably increasing the mature size or birth weight of the breed. It is however apparent from Figure 1.4 that both the breeding values for age at first calving (AFC) and inter-calving (ICP) period of the Bonsmara breed have increased since 1990. The reproductive ability of the Bonsmara, therefore, decreased during the same period in which progress was made in terms of growth. Improving the reproduction efficiency of the Bonsmara breed should therefore be a priority for the elite Bonsmara breeders. A better understanding of the influence that that the environment has on the reproductive ability of Bonsmara cows should also be valuable for improving the reproductive ability of the breed.

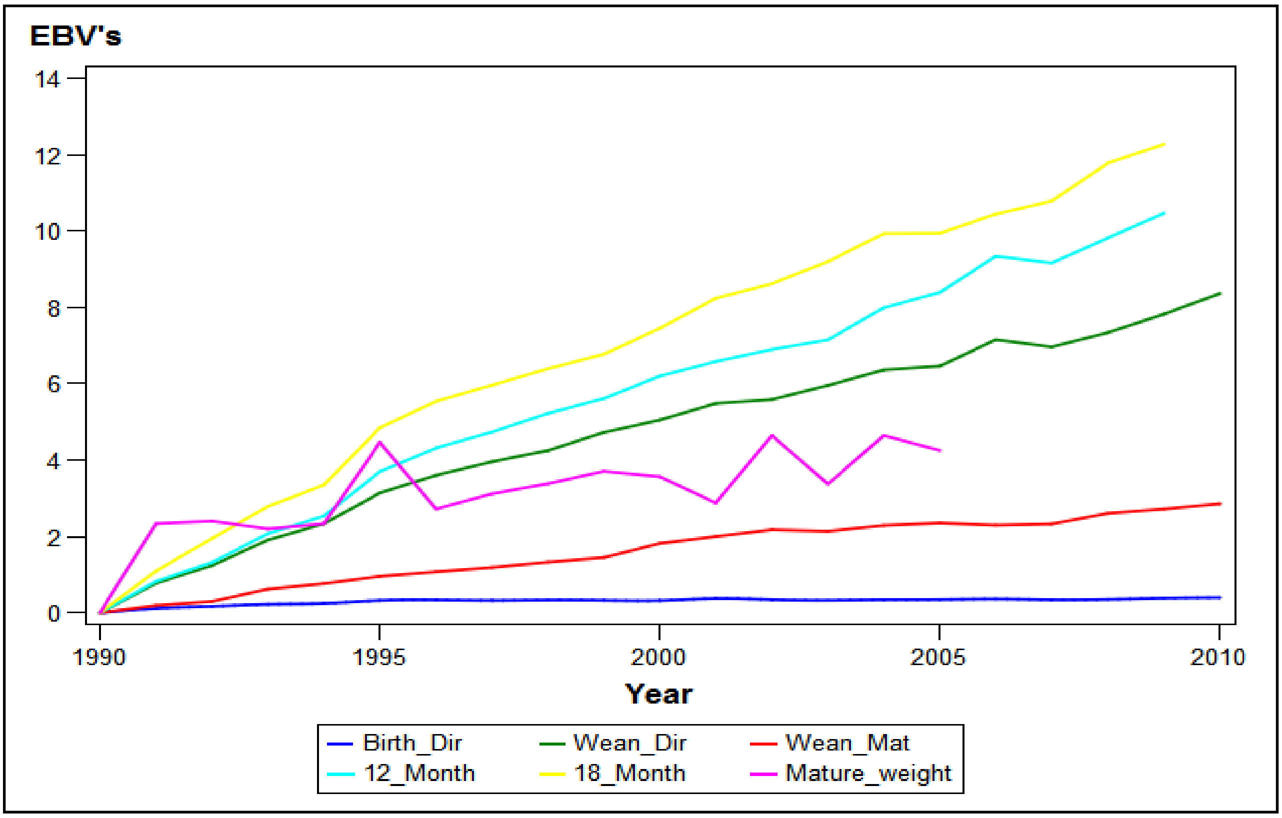

Figure 1.3 EBV trends for growth traits of the Bonsmara breed. Source: ARC-API

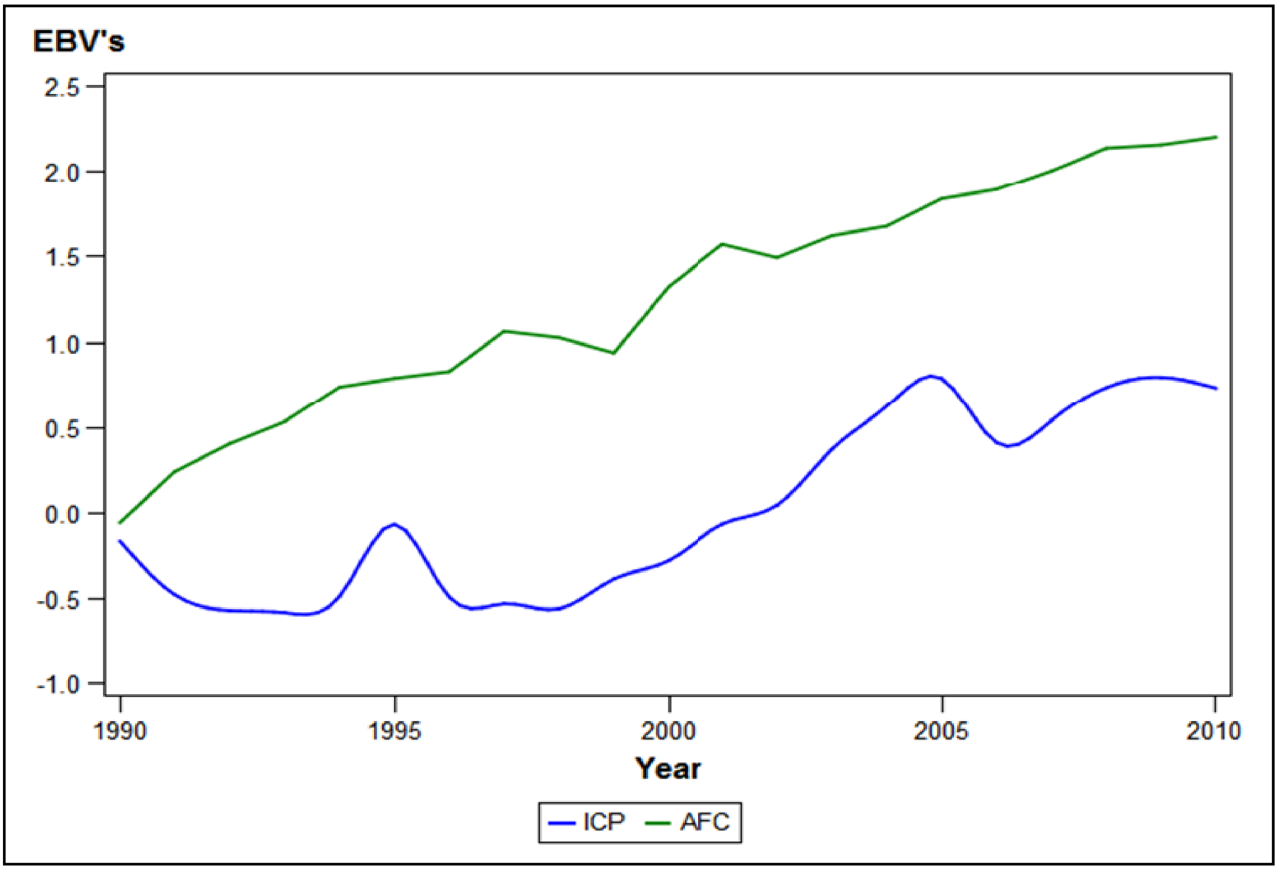

Figure 1.4 EBV trend for reproduction traits in the Bonsmara breed. Source: ARC-API

1.2. AIM OF THE STUDY

The aim of this study was to investigate the influence of the production environment on the production efficiency of Bonsmara cows in South Africa. For simplicity's sake only the major beef production traits (growth, size and reproduction) were used as components of production efficiency. A number of research objectives were investigated to achieve the overall aim of the study. The objectives were to.

1) Identify a classification system that describes the beef production regions of South Africa;
2) Quantify the influence of production region on the production traits of Bonsmara cows;
3) Quantify the influence of the combined environmental characteristics on the production traits of Bonsmara cows;
4) Quantify the influence of individual environmental characteristics on the production traits of Bonsmara cows; and
5) Quantify the relationship between the mature size and reproduction efficiency of Bonsmara cows.

CHAPTER 2
LITERATURE STUDY

2.1. THE SOUTH AFRICAN BEEF PRODUCTION ENVIRONMENT

A large portion of the South African production environment is arid or semi-arid (Schulze, 1997), with high ambient temperatures that often pose a heat threat to livestock production during summer (Du Preez *et al*., 1992; De Jager, 1993). The natural grazing is frequently the only feed source (Snyman, 1998) and insufficient intake of nutrients is often the most important constraint in beef production in South Africa (De Waal, 1990). The South African beef industry is, therefore, dominated by extensive production systems because of these environmental constraints (Scholtz *et al*., 2008).

The classification of a production environment can provide an indication of the value of the region for livestock production (Tainton *et al*., 1993). Extensive production environments are classified in South Africa based on both the general structure and composition of the prevailing vegetation or on the seasonal use classes based on the quality of the forage the environment produces (Tainton *et al*., 1993). The structure and composition of the vegetation give an indication as to what livestock the environment is suited for while the seasonal quality of the forage indicates which management is needed in the region (Tainton *et al*., 1993). Internationally a number of agricultural mapping classification systems have been proposed by various researchers (Notenbaert *et al*., 2009). The main classification systems that have been compiled from integrated data from crop production, the animal-land relationship, intensity of production, and type of product produced (Notenbaert *et al*., 2009). Classification systems for other criteria include size and value of livestock holdings, distance and duration of animal movement, types and breeds of animals kept, market integration of the livestock enterprise, economic specialisation and household dependence on livestock (Notenbaert *et al*., 2009).

The earliest South African environmental classification systems were published by Acocks (1953). The classic Acocks veld-type map was first published in 1953 and subsequently updated in 1988. The Acocks veld-type classification system was based on the agricultural potential of the vegetation (Acocks, 1988). Following Acock's, (1953) publication, Bonsma & Joubert (1957) published their natural livestock production region classification system in 1957. Their livestock-production areas of South Africa map, which is shown in Figure 2.1, identified the production regions suitable for different types of livestock. The classic Acocks (1988) vegetation classification system was later replaced by that of Low & Rebelo (1996), who followed a more modern approach to vegetation mapping (Low & Rebelo, 2000). The older mapping techniques were based on syntaxonomy (vegetation system systematics) that provides a classification system of vegetation in a mapped area (Mucina & Rutherford, 2006). The more modern vegetation mapping techniques work on a much broader platform by incorporating new approaches of remote sensing and spatial environmental correlation by GIS (Alexander & Millington, 2000). VEGMAP is the latest South African vegetation classification system and was introduced by Mucina & Rutherford in 2006. VEGMAP was compiled with the help of geographic information system (GIS) tools and incorporated aerial photography and satellite imagery in combination with traditional field-based ground-truthing (Mucina & Rutherford, 2006).

The only South African environmental classification system that was specifically intended for livestock production was the livestock-production areas map of Bonsma & Joubert (1957). To delineate their livestock-production areas Bonsma & Joubert (1957) used those factors they considered as having an influence on livestock production. Bonsma & Joubert (1957) considered the hereditary differences between the characteristics that determine the productivity of certain types of livestock. These researchers accounted for the physiological phenomena of growth, development and reproduction and the different nutritional requirements of different classes of livestock. They also accounted for the geographical and physical features of the livestock-production regions and their potential to provide favourable nutritional conditions to promote the optimal expression the animal's productive ability.

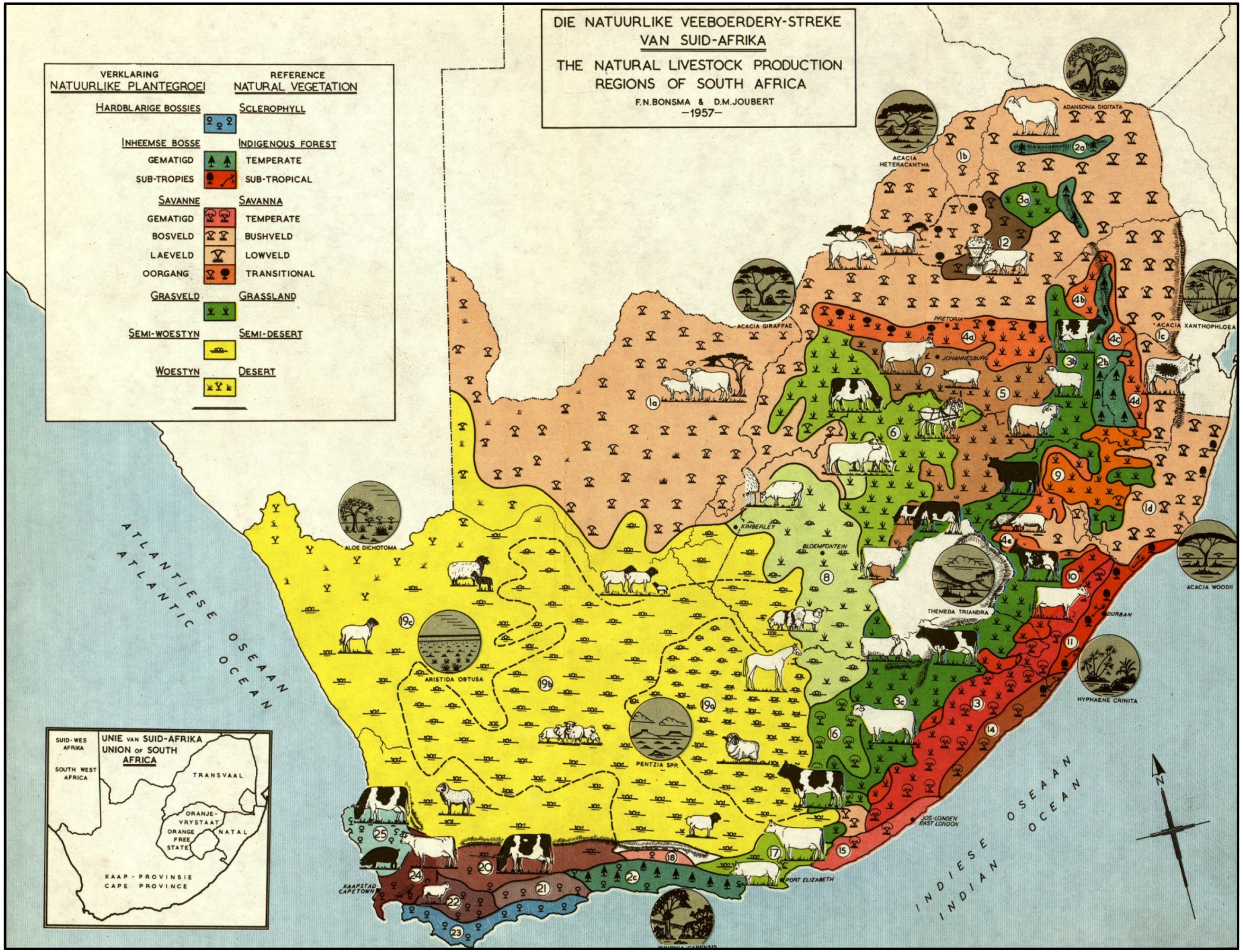

Figure 2.1 The natural livestock production areas of South Africa, according to Bonsma & Joubert (1957)

2.2. INFLUENCE OF THE ENVIRONMENT ON BEEF COW EFFICIENCY

There is no universally accepted definition of beef cow efficiency in the literature. Dickerson (1970) defines an efficient cowherd as being sexually precocious, with a high reproductive rate, low dystocia and longevity with minimum maintenance requirements. According to Dickerson, a herd's ability to reproduce in a given nutritional environment is the most important contributing factor to efficiency. A more recent definition of an efficient beef cow is that of Johnson *et al.* (2010) who define the most efficient beef cow as the one with the highest milk production that can yearly wean a calf with the growth and carcass characteristics required by the market. The different avenues that exist to increase the cost efficiency of a beef herd by 20% were indicated by Roux (1992). The avenues are presented in Table 2.1.

Table 2.1 Gain in herd cost efficiency for a 20% gain in a component of beef production (Roux, 1992; Van der Westhuizen, 2009)

Component	% Gain	Achievability
Replacement rate	3-5	Medium
Surplus reproduction rate	8-10	Medium
Fertility at first mating		
5 matings	2	Medium
10 matings	1	Medium
Sire/dam line mature weight		
Favourable complete dominance	6-7	Easy
Additive gene action	3-4	Easy
Sexual dimorphism	6	Medium
Feeder-breeder growth manipulation	9	Easy
Growth feed efficiency (conception to % max. size)	11	Hard
Maintenance & lactation feed efficiency: Female herd	8-10	Hard

From Table 2.1 it can be concluded that overall herd production efficiency can be achieved by increasing the efficiencies of the different component traits. The challenge, however, is to maintain a balance when setting breeding objectives and selection criteria by keeping the relationship between traits in mind (Van der Westhuizen, 2009)

The environment is known to have a large influence on livestock production (Hafez, 1968; Bonsma, 1983). The environment's influence on livestock production can be direct, through effect on the animal's physiology, or indirect, through influences on the feed sources. In extensive production systems cattle are dependent on the natural forage for the majority of their nutritional needs (De Waal, 1990). The climate of an environment affects vegetation and, therefore, grazing in Southern Africa both directly and indirectly. Direct influence occurs through solar radiation, temperature and moisture, which have an influence on the distribution of the plant species. Indirect influences occur through the climate's influence on soil conditions and fire regime (Schulze, 1997). The main climatic factors that influence animal production have been identified as high temperatures and humidity, as well as solar radiation and altitude (Yousef *et al.*, 1968; Bonsma, 1983).

The most important constraint on cattle production on rangeland is insufficient intake of digestible nutrients in relation to the animal's requirements (De Waal, 1990). This constraint may at times be aggravated by deficiencies of specific nutrients in the herbage (De Waal, 1990). The nutritional value of the diet of a grazing ruminant is determined by the nutritive value, digestibility and intake (Meissner *et al.*, 1999). The nutritional value and digestibility of the forage is determined by the plant's chemical composition, which is the result of the plant metabolism type, species, stage of growth, season, sunlight, soil nutrient status and acidity, available moisture, and ambient temperature (McDonald *et al.*, 2002). Intake is linked to digestion (fermentation) rate. When intake is not limited by the digestibility of the feed, it is influenced by availability, palatability, moisture content and forage management (Meissner *et al.*, 1999).

The production capacity of rangeland is influenced by a number of factors including plant composition (Snyman, 1999), rangeland condition (Snyman, 1999), temperature (Tainton & Hardy, 1999), the annual variation and distribution of rainfall (Snyman, 1998) and soil fertility (Scholes, 1990). All these factors invariably influence animal production (De Waal, 1990). Cattle production in South Africa is consequently mostly influenced by the environmental conditions such as rainfall, temperature and nutritional factors, as well as an excess or lack of minerals.

2.2.1. Climate

The major climatic processes are rainfall and temperature. These processes have a direct and an indirect influence on animal production. Animal production is influenced directly through physiological interactions (Hafez, 1968) and indirectly through the climates influence on forage production (Snyman, 1998).

Rainfall

Approximately 65% of South Africa's rangeland is arid or semi-arid with a mean annual rainfall of 500 mm or less (Schulze, 1997). In these areas where annual or seasonal droughts are an inherent climatic characteristic, rangeland is often the only source of feed and is seen as an asset for the extensive livestock industry (Snyman, 1998).

Rainfall has a significant influence on forage production and hence has an indirect influence on animal production. Rainfall has both a long- and short-term influence on animal production. The long-term effect of rainfall is mainly through its effects on soil fertility Scholes (1990) and vegetation distribution (Schulze, 1997). Dystrophic (infertile) soils are more common in higher rainfall regions and eutrophic (fertile) soils in drier localities (Hunsley, 1982). There are, however, quite a number of exceptions to this rule (Scholes, 1990). Rainfall influences vegetation distribution and production through its magnitude, distribution, variability and concentration (Schulze, 1997).The rainfall season has a large influence on species distribution, with tropical and subtropical species dominating the northern summer rainfall areas of South Africa and temperate species occurring in the winter rainfall biome of the Western Cape (Tainton & Hardy, 1999).

The short term influence of rainfall on animal production is well recorded. The South African rangeland production is primarily driven by rainfall (Palmer & Ainslie, 2006). Growth performance is known to have a curvilinear relationship to rainfall (Fynn & O'Conner, 2000). Although the total seasonal rainfall contributes to the production potential of vegetation within a given area, it is the seasonal distribution of the rainfall that determines the fodder flow within a given season (Snyman, 1997).

Temperature and humidity

Environmental temperatures have a direct as well as an indirect influence on animal production. High summer temperatures are of major concern in South African livestock production systems (Bonsma, 1983; Du Preez *et al*., 1992). The temperature humidity index (THI) described by Thom (1959) has been widely used as an indicator of thermal stress in livestock and forms the basis of the Livestock Weather Safety Index developed by the Livestock Conservation Institute (LCI, 1970).The Livestock Weather Safety Index defines thresholds based on the severity of heat events. THI values ≤ 74 are classified as alert; $74 < \text{THI} < 79$ as danger; and $79 \leq \text{THI} < 84$ as emergency (Amundson *et al*., 2006).

In South Africa, the heat risk expands progressively from the north-western areas of the country, covers most of the country almost entirely during the month of January and then progressively contracts and reaches zero during July (Du Preez *et al*., 1992; De Jager, 1993). The physiological responses of cattle to acute periods of excessive heat stress include increased respiratory rate, decreased feed intake, increased water intake, and imbalances in blood gases and plasma electrolytes (Yousef *et al*., 1968; Finch, 1986; Beatty *et al*., 2006). Even a small upward shift in core body temperature has a profound effect on the production and reproductive abilities of cattle (Finch, 1986). It is reported by Amundson *et al*. (2006) that pregnancy rates become negatively affected when the environmental THI rose above 73. The conception rates in Bos taurus cattle declined in temperatures above 23.4 C (Amundson *et al*., 2005).

The prevailing environmental temperature in conjunction with rainfall also has an influence on the distribution of vegetation. The effect of temperature on vegetation is noticeable with the increase in altitude.

Tropical and subtropical species occur in the hotter low-lying coastal areas of the southern and eastern parts of the country, with temperate plants occurring in the colder, higher altitudes (Tainton & Hardy, 1999).

2.2.2. Soil

Soil fertility and forage production

The parent rock determines the elements present in the soil and the nutrient elements that are available for plant use. When plant growth is not inhibited by soil moisture, it is principally controlled by the status of these nutrients (Scholes, 1990). The extent to which elements are retained in the soil is determined by leaching, gleying and other soil chemical properties such as pH and redox potential, as well as the organic acids produced by soil organisms (Whitehead, 2000).

Usually only a small proportion of the soil's nutrient element content is available for plant absorption at any one time. The soluble fraction is mostly available in simple ionic form, although a small portion consists of simple organic compounds. Many nutrient elements in the soil also occur in more than one chemical compound. Speciation varies with factors such as pH, redox potential and the occurrence of complexing agents (Whitehead, 2000). Nutrient element comparison between plants and the soil in which they grow shows a large variation in nutrient content (Whitehead, 2000). Although there is a consistent variation in the concentration of some nutrient elements between species, the differences between species that grow under uniform conditions are usually much smaller than the differences within individual species grown under a range of different environmental conditions. The factors that contribute to the variation of elements in herbage concentrations include maturity of the herbage, species differences, seasonal variation, climatic conditions and soil type (Whitehead, 2000).

The soil factors that have the largest influence on the availability of nutrient elements for plant absorption are cation exchange capacity (CEC), soil pH, soil carbon content and redox conditions (Whitehead, 2000). The inherent soil properties have a large influence on the chemical composition of the plant (Kumaresan *et al*., 2010) and would consequently have a similar effect on the plant's nutritional value.

CEC

CEC is the sum total of exchangeable cations that any soil can absorb. The CEC is an important chemical property of soil that is used for assessing its fertility and environmental behaviour. CEC tends to increase with an increase in pH and organic soil matter (Brady & Weil, 2002a). Soil CEC is largely influenced by the negatively charged sites of clay minerals and organic soil matter. Cations are absorbed to balance the negative charges and can be replaced by other cations in solution through cation exchange (Whitehead, 2000). Cation exchange takes place when another cation with an equal charge exchanges place with the first ion at the exchange complex. The nutrient cation is then forced into the soil solution, where it can be assimilated by roots or soil organisms or is removed by leaching (Brady & Weil, 2002c).

The greater the CEC of a soil the greater its ability to retain its nutrient cations in a form that is potentially available for plant and microorganism absorption (Whitehead, 2000). Soils with a high CEC is also not readily susceptible to leaching (Whitehead, 2000). The soils of southern Africa are classified as dystrophic types with exchangeable cation levels of less than $5cmol_c/kg$, eutrophic types with levels of greater than $15cmol_c/kg$, and mesotrophic types with intermediate soil cation ranges (Mac Vicar, 1977).

Soil pH

Soil pH is a measure of the acidity or alkalinity of the soil. Soil pH is a major variable that influences soil properties and, thus, plant species composition. Soil pH has an influence on the soil's chemical and biological properties as well as the soil's physical properties because the pH of the soil has an influence on the dispersion of clays and the formation and stabilisation of aggregate structures, which in turn has a major influence on the movement of water and air. Soil pH also influences the availability of nutrients to plants and soil microbes (Brady & Weil, 2002a).

Acidification is a natural process in soil formation. It occurs when the soil processes that produce H^+ outpace the processes that consume the available H^+. Natural acidification is largely driven by the production of carbonic and other organic acids and the leaching of cations like Ca, Mg, K and Na which is replaced in the exchange complex by the H^+ ions from the acids. Acidification is more prevalent in humid regions with a high rainfall and is less marked in drier regions (Brady & Weil, 2002a).

Soil pH has different effects on the availability of plant nutrients. Generally the availability of micronutrients occurring as cations especially Al, Fe, Mn, and Co tend to increase with increasing soil acidity whereas the availability of the micronutrients occurring as anions (B, Mo, and Se) tends to decrease with increasing acidity. Very low soil pH inhibits plant root growth and microbial activity (Whitehead, 2000).

Soil organic matter

Soil organic carbon and total nitrogen in the soil is a simple measure of the soil's organic matter content (AGIS., 2010), and is the central factor that influences soil quality (Snyman, 1998) and also provide much of the CEC and water holding capacity of soils (AGIS., 2010). The soil's organic matter also has an influence on the formation and stabilisation of soil aggregates (Brady & Weil, 2002b). Most of the N, P and S in soils occurs in its organic content. The availability of these elements to plants is expedited by microbial enzymes (Whitehead, 2000).

Climate, drainage and vegetation type determine the level of soil organic matter (Brady & Weil, 2002b). Rangeland degradation decreases soil organic matter content (Du Preez & Snyman, 1993; Du Preez & Snyman, 2003). Reduced plant production increases soil erosion (Snyman, 1998) and change in soil climate and can also lead to the loss of soil organic matter (Snyman & Du Preez, 2005). Soil organic matter is higher in cool moist environments and lower in hot, dry areas (Brady & Weil, 2002b). A high level of organic matter supports a large microbial biomass, thus a rapid rate of decomposition, which releases an adequate amount of N, P and S for plant use (Whitehead, 2000).

2.2.3. Forage

The characteristic of rangeland production that has the largest influence on livestock production in South Africa is the season of use and grazing capacity (Tainton, 1999).

Season of use

The terms "sweet"-, "mixed"- and "sourveld" refer to the period of the year in which the natural grazing can sustain animal production without supplementation (Tainton, 1999). Season of use also gives an indication of the type of production system that is suitable for the area (Snyman, 1997).

"Sweetveld" is defined as natural rangeland in which the forage plants retain their acceptability and nutritive value after maturity and can therefore be utilised throughout the year (Tainton, 1999). As the translocation of nutrients from the leaves to the roots in the winter is minimal, the animals on sweetveld remain in good condition. Sweetveld generally occurs in the summer rainfall area, at low elevation, usually, but not always, in frost-free areas that receive 200-500 mm of rain per annum. It is mostly associated with soils with a high base status (Van Rooyen, 2002; Tainton, 1999) and tends to be eutrophic (nutrient rich) (Scholes, 1990). Sweetveld can also occur in areas where the rainfall is erratic but throughout the year and generally has a low carrying capacity (Smith, 2006). The production of livestock on sweetveld is limited by forage quantity (Tainton, 1999). Sweetveld is sensitive to overgrazing but recovers faster than sourveld (Smith, 2006).

"Sourveld," on the other hand, is defined as natural rangeland in which the forage plants become unacceptable and less nutritious after maturity and can thus be only be optimally utilised for a certain portion of the year unless supplements are supplied (Tainton, 1999). Sourveld is usually long grasveld (Smith, 2006). Translocation of nutrients to the roots occurs towards the end of the growing season, and sourveld can therefore only maintain animals for six to eight months of the year. It occurs mostly in the high-lying montane areas, with cold winters and a rainfall higher than 650 mm per annum. It is associated with soils with a low pH (Van Rooyen, 2002; Van der Westhuizen, 2008). Sourveld soil is usually dystrophic (nutrient poor) (Scholes, 1990). The production of livestock on sourveld is limited by forage quality (Tainton, 1999). Sourveld can tolerate moderate overgrazing but this will lead to lowered forage production (Smith, 2006).

Mixed veld is intermediate between these two types and ranges from sweet-mixed to sour-mixed veld, depending on soil type and plant species composition (Tainton, 1999). Mixed veld usually occurs in the transitional area between sweet-and sourveld (Van Rooyen, 2002). It varies between sweet-mixed that provides grazing for nine to eleven months of the year to sour-mixed that provides grazing for six to eight months of the year (Smith, 2006).

Although attempts have been made to classify all South African veld-types into the above-mentioned classes, the subject of sweet and sourveld classification is still very controversial (Tainton, 1999). There is, therefore, unfortunately, no current national database on this issue. (P. Avenant. DAFF. Personal Communication. Cnr Annie Botha and Union Street, Riviera, Pretoria. 2010). A broad indication of the distribution of the season use class types was given by Tainton (1999) and is indicated in Figure 2.2.

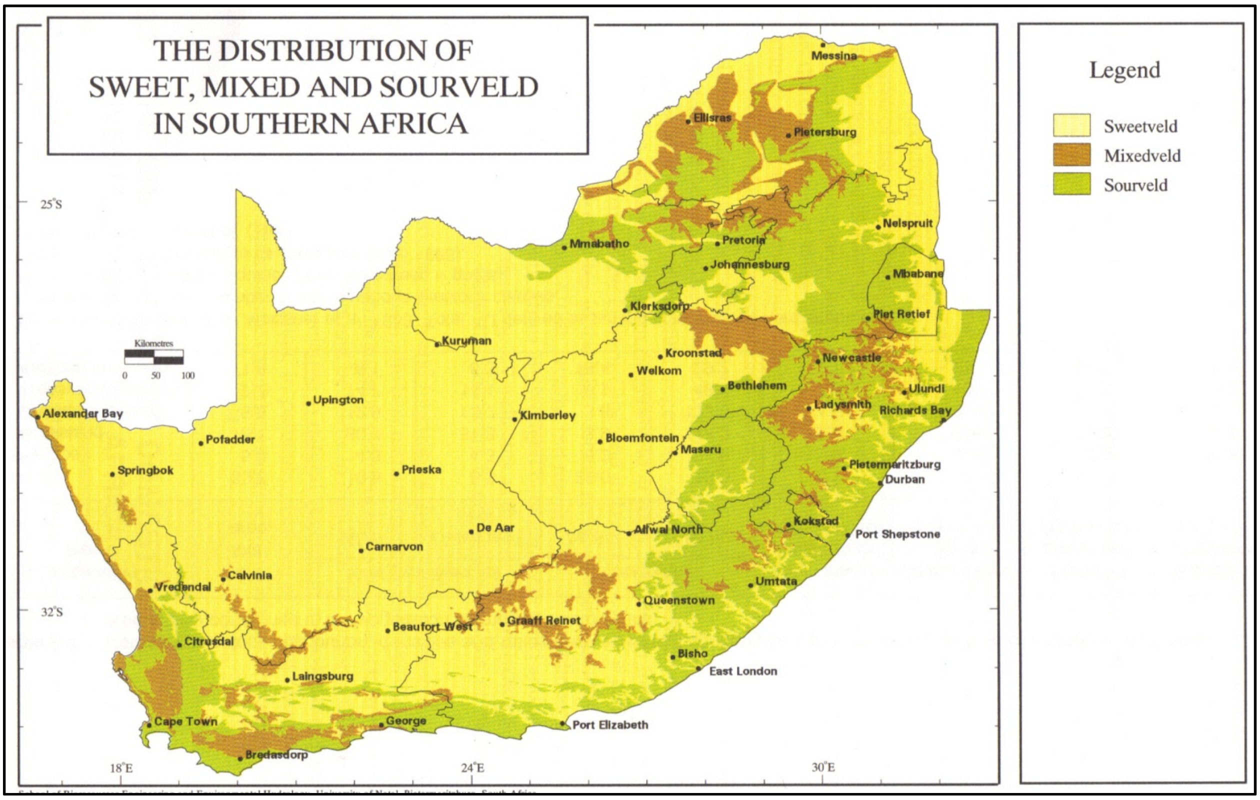

Figure 2.2 The distribution of sweet, mixed and sourveld in South Africa (Tainton, 1999)

Grazing capacity

Grazing capacity is the productivity of the grazeable portion of a homogenous unit of vegetation expressed as the area of land required to maintain a single animal unit over an extended number of years without deterioration in the vegetation or soil (Tainton, 1999). It is difficult, but essential, to determine grazing capacity, otherwise rangeland can not be utilised in an optimal and sustainable way (Van der Westhuizen *et al*., 2001a). Grazing capacity is used to determine the rate at which rangeland should be stocked. The stocking rate has an immediate effect on the quantity of forage available, thereby affecting intake and animal performance (Morris *et al*., 1999). Stocking rate is the single operator dependent variable that has the greatest influence on the biological output of saleable products (Snyman, 1997).

Grazing capacity is a compound measurement based on a number of environmental characteristics such as rainfall, available soil moisture, soil depth and evapotranspiration, rangeland condition, topography and stock type (Fourie, 1985). A change in any of these factors will cause a change in the grazing capacity (Van der Westhuizen *et al*., 2001a). The grazing capacity of any specific area changes continuously from veld-type to veld-type, season to season and year to year. To compile an accurate grazing capacity map the long-term grazing capacity of the area should be known (Lubbe, 2005). The determination of grazing capacity is controversial, a number of theories exist and various methods are used to determine grazing capacity, but there is not one is universally used or accepted (Roe, 1997). The grazing capacity will obviously change whenever any of its components does (Van der Westhuizen *et al*., 2001a). In South Africa the determination of grazing capacity is approached in two different ways: the agronomic approach is based on weighed palatability composition scores and potential dry matter production, whilst the ecological approach makes use of the characteristics of the vegetation and the composition score, basal cover, topography and soil erodibility of the site (Hardy *et al*., 1999).

Vegetation composition

The species composition of the vegetation has an influence on animal production through its influence on the quality of the forage and the intake. Species composition affects intake at two levels. It could affect the potential rate of intake due to differences in bite size and biting rate due to differences in plant morphology or through the time required to find different species in the sward (Hardy *et al*., 1997). It also appears as if the vegetation composition of the rangeland influences the species composition of the diet, which has an influence on the nutrient intake of the diet of the grazing ruminant (Hardy *et al*., 1997). Species composition appears to be important in humid sourveld regions due to the inherent quantity and quality of the forage (Hardy *et al*., 1997). It does, however, not appear to have any influence on the nutritional intake of the grazing ruminant in sweetveld (Hardy *et al*., 1997).

2.2.4. Minerals

Cattle grazing on natural pastures and not supplemented are dependent on the forage for their main source of minerals (McDowell, 1996). Specific nutrient deficiencies would therefore influence cattle production in South Africa (De Waal, 1990). The composition of plant nutrients varies with the species, plant maturity, season, weather and soil type (Whitehead, 2000). Most of the known naturally occurring mineral deficiencies in cattle can be associated with specific regions with specific soil characteristics (McDowell, 1996). Soil analysis is therefore important to thoroughly understand one of the factors affecting livestock health and productivity of cattle on natural grazing (Trengrove, 2000).

Phosphorus

It is widely accepted that forage produced on rangeland in South Africa is often deficient in P (Du Toit *et al*., 1940; Meissner, 1999). P deficiency is associated with subnormal growth in young animals and low live weight gain in mature animals. Low dietary intake of P is also associated with poor fertility and lowered milk production (McDonald *et al*., 2002). The determination of the source of poor livestock performance is not always easy. The test of any limiting nutrient would, however, be improved animal performance following supplementation (Read *et al*., 1986).

A great deal of research has been done on the influence of P-supplementation in different areas of South Africa. The groundbreaking work of Arnold Theiler in the early part of the previous century regarding P deficiency is very well known (Theiler, 1912; Theiler *et al*., 1927). At Armoedsvlakte in the North West province Read *et al*. (1986) and De Waal *et al*, (1996) found severe P-deficiency in cattle. They found that P deficiency causes depressed feed intake, stunted growth, high mortality rates and poor reproductive performance. At Glen in the central Free State province Read *et al*. (1986) found, on the other hand, no advantages in any aspect of animal performance with P-supplementation. At Potchefstroom in the North-West province De Brouwer *et al*. (2000) also found no differences in conception rates between treatment groups. However P-supplemented cows were heavier than un-supplemented cows and some of the un-supplemented cows died of emaciation due to aphosphorosis. At the Mara Agricultural Research Station Orsmond (2007) showed that in a trial done in two different veld-types that there was no difference in cow reproduction with P-supplementation, but an increase in weight occurred in supplemented cows.

It therefore seems that P supplementation produces different animal responses in different environments. The response to enhanced P nutrition must therefore be the result of a number of reasons. Unfortunately, none of the researchers seemed to have done any soil analyses. The different responses might for instance have been due to a lack of protein or energy, not P, in their diet, the availability of P in different forage species or the interaction of P with other elements/minerals such as Ca, Cu, or the original P-status of trial animals could also be responsible for the different reactions to P-supplementation (Karn, 2001).

2.3. COMPONENTS OF BEEF COW EFFICIENCY

2.3.1. Adaptation

According to classic research by Bonsma (1983), one of the characteristics of highly efficient cattle is their ability to adapt to and reproduce in their environment. Bonsma postulated that the ability to adapt is due to physiological mechanisms that decrease the negative influence of environmental stressors. There are two types of physiological regulation — homeostasis and homeorhesis (Collier *et al*., 2005).

Homeostasis and homeorhesis

The overall goal of these mechanisms regulating animal physiology is to maintain the animal's well-being regardless of the physiological situation or environmental challenges that are encountered (Collier *et al*., 2005). Homeostasis is defined by the International Commission for Thermal Physiology as "the relative constancy of physiochemical properties of the internal environment of an organism as being maintained by regulation" (ICTP, 2001). The best known example of a homeostatic mechanism is the maintenance of circulating glucose to peripheral tissues by means of the hormones insulin and glucagon (Collier *et al*., 2005). Homeorhesis is defined by Bauman & Currie (1980) as being "the orchestrated or coordinated control in metabolism of body tissues necessary to support a physiological state". The use of the definition of homeorhesis has since expanded to include different physiological states, nutritional and environmental situations as well as pathological conditions. Homeorhetic regulation involves the coordination of physiological processes in support of a dominant physiological state or chronic situation (Collier *et al*., 2005). Lactation is possibly the best example of homeorhesis (Collier *et al*., 2005). Homeorhetic controls are characterised by its chronic nature rather than the acute response characteristic of homeostatic regulation (Bernabuccil *et al*. 2010), and are characterised by the simultaneous influence they have has on multiple tissues and systems, which results in an overall coordinated response, mediated through altered responses to homeostatic signals (Bauman & Currie, 1980; Bernabuccil *et al*., 2010).

Heat stress

Heat stress is a major factor in South African livestock production systems (Bonsma, 1983; Du Preez *et al*., 1992). All homeotherms have a thermo neutral zone where temperature regulation is achieved only by control of sensible heat loss; i.e., without regulatory changes in metabolic heat production or evaporative heat loss (ICTP, 2001). When environmental variables such as ambient temperature, humidity, air movement and solar radiation combine to reach values that surpass the upper limit of the thermo neutral zone, the affected animal enters a condition known as "heat stress" (Bernabuccil *et al*., 2010).

It is well known that there are differences in the heat stress susceptibility between species and breeds (Silanikove, 2000; Collier *et al*., 2005). These differences amongst others are due to differences in size, metabolic rate, heat storage capacity, coat and skin between species (Macfarlane, 1968). The ability of the breed or species to lose heat through the respiratory tract, its water deprivation tolerance, sweating ability and kidney structure as well as amount of faecal water excreted and body water content and turnover also have an influence (Macfarlane, 1968). The animal's ability to conserve fat, water and nitrogen also plays a significant role in heat susceptibility (Macfarlane, 1968). Sheep and goats are less sensitive to heat stress than cattle (Silanikove, 2000). This is due to the higher metabolic rate and poor water retention mechanisms of the kidney and gut of the cow (Bernabuccil *et al*., 2010). Dairy cattle are more sensitive to heat than beef cattle, due to their higher endogenous heat production (Bernabuccil *et al*., 2010). The levels of resistance to heat stress also vary among breeds within the same species. Bos Indicus cattle are widely recognised as being more resistant than Bos Taurus cattle (Turner, 1980).

Adaptive mechanisms

Heat stress activates physiological and behavioural responses to reduce the strain of the heat load in an animal by increasing heat loss and reducing heat production, in an attempt to maintain body temperature within normal range (Bernabuccil *et al*., 2010). Acclimatisation is one of these responses. Acclimatisation is a "physiological or behavioural change occurring within the lifetime of an organism that reduces the strain caused by stressful changes in the natural climate" (ICTP, 2001). The process of acclimatisation can take several weeks (Collier *et al*., 2009) and has traditionally been referred to acclimatisation homeostasis (Horowitz, 2002). More recently the process of acclimatisation has been proposed to be a homeorhetic mechanism (Collier *et al*., 2005), as it is thought to be a chronic mechanism and the end result of acclimation is a change in target tissue response to homeostatic signals (Collier *et al*., 2009). The metabolism of an adapted animal therefore changes between seasons (Collier *et al*., 2009).

Heat acclimation appears to be biphasic (Collier & Zimbelman, 2007). It starts with short-term heat acclimation (STHA) that is initiated during periods of heat stress. STHA changes the cellular signalling pathways (Horowitz *et al*., 1996). The changes in the signalling pathways cause a disturbance in the cellular homeostasis that causes a reprogramming of cells to survive the harmful effects of heat stress (Horowitz, 2001). After the STHA phase has been completed and the heat-acclimated phenotype is expressed, long-term heat adaptation (LTHA) takes place (Horowitz, 2001). LTHA is characterised by modified gene expression caused by the heat stress and cellular response resulting in enhanced efficiency of signalling pathways and metabolic processes (Horowitz, 2001).

Our understanding of the metabolic regulation during heat stress is still basic, most of the known examples of metabolic regulation during heat stress cause decreased heat production and increases the animal's ability to dissipate heat more efficiently (Collier & Zimbelman, 2007). The primary hormones influenced by heat stress are the thyroid hormones: prolactin, somatotropin, thyroxine, antidiuretic hormones, glucocorticoids and mineral corticoids (Beede & Collier, 1986; Bernabuccil *et al*., 2010). The thyroid hormones, T4 and T3, are decreased during heat stress in order to reduce endogenous heat production (Horowitz, 2001; Bernabuccil *et al*., 2010). The levels of circulating prolactin are increased during heat stress independent of reduced feed intake (Ronchi *et al*., 2001; Roy & Prakesh, 2007). Prolactin may play an important role in through improved insensible heat loss and sweat gland function (Beede & Collier, 1986). It is currently unknown if increased prolactin levels affect the ability of animals to metabolically adapt during heat stress, but it is important as a homeorhetic hormone (Bernabuccil *et al*., 2010). The influence of heat stress on the somatotropic axis has also not been properly characterised (Collier *et al*., 2005). Conflicting reports have been published on the reaction of somatotropin to heat stress. Some of the older research indicates that somatotropin decreases in heat-stressed animals (McGuire *et al*., 1991) while more recent work by Rhoads *et al*. (2009) suggest that somatotropin levels are not at all influenced by heat stress. Acute heat stress will cause an increase in circulating cortisol, norepinephrine and epinephrine levels that act as catabolic signals to stimulate lipolysis and adipose mobilisation (Alvarez & Johnson, 1973; Collier *et al*., 2005). Increased basal insulin levels and stimulated insulin response are also exhibited by heat-stressed cattle (Wheelock *et al*., 2010). An expanded list of endocrine changes that occur during acclimatisation is presented in Table 2.2.

Table 2.2 Some endocrine adaptations made during heat acclimatisation in cattle (Collier & Zimbelman, 2007; Bernabuccil, *et al*., 2010)

Tissue	Response	Reference
Adrenal	Reduced aldosterone secretion	(Collier *et al*., 1982)
	Reduced glucocorticoid secretion	(Collier *et al*., 1982) (Ronchi *et al*., 2001)
	Increased epinephrine secretion	(Alvarez & Johnson, 1973)
	Increased progesterone secretion	(Collier *et al*., 1982) (Ronchi *et al*., 2001)
Pituitary	Increased prolactin secretion	(Ronchi *et al*., 2001) (Roy & Prakesh, 2007)
	Decreased somatotropin secretion	(McGuire *et al*., 1991)
	No change in somatotropin	(Rhoads *et al*., 2009)
Thyroid	Decreased thyroxine secretion	(Collier *et al*., 1982)
Adipose tissue	Increased leptin secretion	(Bernabucci *et al*., 2006)
Placenta	Decreased estrone sulfate secretion	(Collier *et al*., 1982)
Liver	IGF-I unchanged or increased	(McGuire *et al*., 1991.

Ruminants primarily oxidise acetate as their principal energy source (Collier *et al*., 2009). However when cattle enter a negative energy balance, they are largely dependent on non-esterified fatty acids (NEFA) for their energy requirements. Heat-stressed cattle have altered post-absorptive carbohydrate metabolisms that could not have been predicted based on their energetic state. It therefore appears as if the post-absorptive metabolism of heat-stressed cattle and that of thermal neutral cattle differ markedly, even though they could both be in a negative metabolic state. The difference in post-absorptive metabolism is primarily characterised by an increase in basal and glucose-stimulated insulin concentrations (Collier *et al*., 2009; O'Brien *et al*., 2010). Heat-stressed cows do not appear to mobilise adipose tissue despite a loss of appetite (Rhoads *et al*., 2009). The lack of circulating NEFA increase in the heat-stressed cows is surprising, since heat-stressed cattle have an increase in cortisol, epinephrine and norepinephrine levels (Beede & Collier, 1986). This hormone profile results in lipolysis and adipose mobilisation in thermoneutral cattle (Rhoads *et al*., 2009). It is likely that the increased basal insulin response prevents fatty acid mobilisation, at the same time ensuring glucose uptake (O'Brien *et al*., 2010). Oxidising glucose is more efficient at capturing ATP than the oxidation of fatty acids. Therefore the endogenous heat production of heat-stressed animals is lowered if it oxidises glucose rather than fatty acids (Collier *et al*., 2009; O'Brien *et al*., 2010).

Heat stress and production

It is well known that heat stress has a negative influence on animal productivity (Bernabuccil *et al*., 2010). Heat-stressed animals tend to decrease feed intake and have an altered endocrine status. These changes lead to a reduction in rumination time and a subsequent decrease in nutrient absorption as well as an increase in maintenance requirement (Collier *et al*., 2005). Heat stress leads to a net decrease in the availability of nutrients and a subsequent negative energy balance (Bernabuccil *et al*., 2010). The negative energy balance caused by heat stress and early lactation has different effects on the somatotropic axis (Collier *et al*., 2005). Some of the metabolic changes associated with heat stress are independent of the influence of reduced feed intake (Ronchi *et al*., 2001; O'Brien *et al*., 2010). In heat-stressed dairy cows, reduced nutrient intake accounts for 35% to 50% of the decrease in milk production, while the rest of production losses are the direct result of heat (Rhoads *et al*., 2009). In growing Holstein calves it appears as if reduced feed intake fully explains stunted growth in heat-stressed animals (O'Brien *et al*., 2010). It is therefore as yet unclear how the interaction between the reductions in production can be correlated to either heat stress or lowered feed intake (Bernabuccil *et al*., 2010).

Heat stress and reproduction

The physiological mechanisms deployed by heat-stressed cattle to maintain homeothermy has a negative influence on the reproductive ability of both sexes (Rhoads *et al*., 2009; Bernabuccil *et al*., 2010). In young Holstein bulls summer temperatures significantly influence semen quality (volume of the ejaculate, sperm concentration and motility, number of sperm and number of motile spermatosoa per ejaculate, whereas the volume of the ejaculate and sperm motility was not significantly affected in mature bulls (Mathevon *et al.*, 1998). It appears as if the semen quality of heat-adapted breeds is affected to a lesser degree by high summer temperatures than that of un-adapted breeds. Nichi *et al.* (2006) found that Simmental bull semen had more major defects in the summer than Nellore bulls.

It is well known that heat stress has a negative influence on female reproduction. The biological mechanisms responsible are, however, not completely understood (Rhoads *et al.*, 2009). Oocyte growth and development in heat-stressed cows is influenced by altered progesterone, luteinising hormone (LH) and follicle stimulating hormone (FSH) secretion during oestrous (Ronchi *et al.*, 2001). Embryonic development and survival is also compromised by increased circulation of ghrelin in heat-stressed dairy cattle (Rhoads *et al.*, 2009). Heat stress is also known to increase plasma urea nitrogen (PUN), which has a negative influence on conception rates. The elevated urea concentrations within the uterus may also indirectly affect embryonic development and survival by altering the uterine environment (Rhoads *et al.*, 2009). Heat stress during pregnancy slows down foetal growth and increases foetal loss (Bernabuccil *et al.*, 2010).

2.3.2. Reproduction

Reproduction and calf survival rate are the most important factors that determine the efficiency of a beef herd (Dickerson, 1970; Taylor, 2006). In spite of the importance of reproduction it is generally accepted that in South Africa the calf crop averages between 60% and 65% per annum (Bosman & Scholtz, 2010). The reproduction traits that are most frequently used to evaluate reproduction performance in South Africa by Bonsmara breeders are: AFC and ICP (Van der Westhuizen *et al.*, 2001b; Rust, 2007) as well as the reproduction index (RI) that is calculated by the South African National Beef Recording and Improvement Scheme (SANBRIS) (J. v.d. Westhuizen. Personal Communication. S.A Studbook. P.O. Box 270, Bloemfontein. 2010).

There are many factors that influence the conception rate of a cowherd. Some of these are: plane of nutrition of bulls and cows, the age of the breeding animals, herd health, libido and semen quality of bulls as well as the ability of cows to conceive and maintain pregnancy (Rust, 2007). The reproductive performance of the bull is influenced by its semen characteristics, sexual drive and social interaction with other bulls (Chenoweth, 1999). The reproductive ability of a cow is determined by her performance in terms of a number of different reproductive functions that occur throughout her lifecycle. These functions can be divided into component and aggregate traits. A component trait is a single event, while aggregate traits are composites of more than one reproductive event (Rust, 2007). Some of the component traits that can be measured include time to first oestrus, number of services per conception, pregnancy rate, heifer pregnancy, gestation length, days to calving, AFC, calving date, calving ease, ICP and days open. A combination of these traits are then used to form aggregate traits, such as calving rate, lifetime pregnancy rate, calving success, calf survival and lifetime production (Rust, 2007). Although these traits might reflect an indication of reproductive performance there are unfortunately no completely satisfactory measure/s for reproductive efficiency (Bourdon & Brinks, 1983; Guttierreza *et al.*, 2002). The lack of satisfactory measures of reproduction efficiency are due to the influence that the age structure of the herd as well as the prevailing environmental and management conditions have on reproductive recording (Rust & Groeneveld, 2001).

AFC

AFC is an important reproduction trait for beef cattle producers, since it affects cow size as well as the number and weight of calves produced (Nunez-Dominguez *et al.*, 1991). AFC also affects the potential annual genetic progress for stud farmers due to the influence of the trait on the generation interval of a herd (Nunez-Dominguez *et al.*, 1991). AFC encompasses puberty, the ability to conceive, gestate, and deliver a calf (Bormann & Wilson, 2010). Any environmental characteristcic that influences any of the above-mentioned factors can influence the AFC of a heifer. It is important to note that the expression of AFC is also limited by the breeding season, the season in which the heifer is born and the season in which she is bred (Bormann & Wilson, 2010).

Beef heifers are generally managed to calve for the first time at either two or three years of age (Nunez-Dominguez *et al.*, 1991; Van der Merwe & Schoeman, 1995). Earlier mating of heifers is however, sometimes associated with an increase in dystocia (Laster *et al*., 1973). There are conflicting reports in the literature regarding the lifetime production span of early mated heifers. Some authors reported an increase in both the number of calves and weaned kilograms (Meaker *et al*, 1980; Nunez-Dominguez *et al*., 1991). Others report that even though an extra calf might have been weaned, there was no increase in the weaned weight (Van der Merwe & Schoeman, 1995). However, it is apparent that the success of mating heifers at 12-months of age depends on nutritional and management levels (Van der Merwe & Schoeman, 1995). Most heifers have the potential to reach puberty and breed satisfactorily as yearlings if given adequate nutrition and are managed properly (Martin *et al*., 1992).

There is controversy in the literature regarding the use of AFC as a measure of female reproductive ability. There are however consensus that there is no alternative reproductive measurement that can be used as a reproductive measure in heifers. From a recording viewpoint, the biggest advantage of AFC is that it can be easily recorded because the birth date of the cow and its first calving date are generally known (Rust, 2007). AFC, however, represents only a single component in the reproductive life of a cow (Rust & Groeneveld, 2001). In a review by Rust & Groeneveld (2001) on breeding objectives for Southern African beef cattle, it was concluded that, in a variable seasonal environment, management decisions have a greater effect on AFC than genetic merit. These authors therefore concluded that under South African conditions, AFC would not be a useful trait for predicting female reproductive performance.

Other researchers such as Silva *et al*. (2005) also object to the use of AFC as a selection criterion for reproduction efficiency. These authors argue that AFC and the probability of heifers to reconceive are determined by different genes. Selection for AFC will thus not always result in sexual precocity. Their conclusion is based on the negative (-0.32) correlation between AFC and heifer pregnancy rate (pregnancy at 16 months) observed in Nellore heifers. Bormann & Wilson (2010) found a large, negative (-0.85) correlation between calving date and AFC in Angus heifers. Selection for AFC may, therefore, favour heifers that are born later in the season (Bormann & Wilson, 2010).

Despite the limitations of AFC it is a useful measure of reproductive performance. The heritability of AFC in the Bonsmara breed is moderate (0.23) (Van der Westhuizen *et al*., 2011) while Rust (2007) found the heritability of AFC as in Drakensberger (0.30) and Afrikaner (0.27) cattle. Genetic progress is therefore possible in AFC through selection. Guttierreza *et al*. (2002) found a high correlation between the AFC and the age at subsequent calving, as well as between the age at calving and the interval between subsequent calvings. These authors suggest that AFC appears to be a crucial trait in the reproductive life of the dam as selection for a shorter AFC could lead to an improvement in calving intervals. Boligon *et al*. (2010) showed that the inclusion of AFC in a selection index should improve the reproductive performance of females. These authors also illustrated that this trait showed little genetic association with mature weight and could be useful in herds that need a constant mature female weight. Grossi *et al*. (2009) illustrated that female growth-related traits (body weight 365 days and body weight 450 day) presented favourable genetic correlations with AFC (0.38 and 0.33 respectively). This could be interpreted that selection for body weight at those ages favours shorter AFC terms. Grossi *et al*. (2009) however attribute the correlations to non-genetic factors, because of the low magnitude of direct heritability estimates for AFC on the farms in the trial. It was argued by Meaker *et al*. (1980) and Van der Merwe & Schoeman (1995) that reducing the AFC is one of only a few means of improving lifetime production efficiency in the beef cowherd. Shorter AFC values naturally reduce the generation interval, and thus contribute to the annual genetic gain of the herd (Grossi *et al*., 2009). Another common but erroneous belief is that scrotal circumference in yearling bulls may be an indicator of reproductive fitness in female offspring (Smith *et al*., 1989; Martin *et al*., 1992). Scrotal circumference was, therefore, often included in selection programmes to improve heifer fertility. However, the statistical association between scrotal circumference and heifer fertility traits are low in more recent datasets (Cammack *et al*., 2009; Grossi *et al*., 2009).

ICP

ICP or calving interval is an aggregate reproductive trait, composed of more than one reproduction event and is defined as the time that elapses between two successful calvings (Rust & Groeneveld, 2001). ICP is regarded as an important fertility trait (Medina *et al*., 2009) and the average ICP of a beef herd should ideally be less than 365 days (Montiel & Ahuja, 2005; Cammack *et al*., 2009). A cow should, therefore, conceive within approximately 80 days after calving (Arthington & Kalmbacher, 2003). It is, however, generally accepted that the ICP in most breeding herds is more than 365 days in the tropical or subtropical areas due to high humidity and temperature and lower forage quality (Arthington & Kalmbacher, 2003). According to the SANBRIS, the current ICP average for the different breeds ranges between 398 – 477 days. The Hereford and Shorthorn breeds have the shortest (398 days) and the Hugenoot breed the longest (477 days) ICP. This data excludes the miniature Dexter beef breed with an ICP of 367 days. The average ICP of the Bonsmara breed is 405 days (Scholtz *et al.*, 2010).

The use of ICP as a measure of reproductive efficiency in a fixed breeding season has been questioned by several authors (Bourdon & Brinks, 1983; MacGregor & Casey, 1999; Rust & Groeneveld, 2001). The major criticism against ICP as a selection criterion for reproductive performance is the negative correlation that exists between ICP and previous calving date, as well as the large influence that the previous calving date has on the ICP (MacGregor & Casey, 1999). The negative correlation between ICP and calving date means that cows that calve early in the season have the longest ICP while those that calve late in the season have the shortest ICP (MacGregor & Casey, 1999).

Heritability estimates for ICP in Bonsmara cattle are respectively 0.08 (ICP1), 0.11 (ICP2) and 0.10 (ICP3 (Van der Westhuizen *et al*., 2011). Other researchers have found heritability estimates ranging from 0.02 (Lopez de Tore & Brinks, 1990) to 0.12 (Guttierreza *et al*., 2002) with a low repeatability of 0.14 (Lopez de Tore & Brinks, 1990). The repeatability estimate for ICP suggests that female culling based on first calving interval is not accurate and there is a risk of culling animals with other desired traits (Azevedo *et al*., 2006). Selection for shorter ICP's could result in indirect selection for a later age of puberty as cows with the shortest calving interval, are often those who calved late in the season (Bourdon & Brinks, 1983). When the ICP of a herd is determined the information from the first parity or the end of a cow's life span is also not taken into account (Rust & Groeneveld, 2001).

Postpartum anoestrus (PPI) is the period after parturition during which cows do not show behavioural signs of oestrus (Montiel & Ahuja, 2005). PPI is caused by static ovaries, where follicular development may take place but none of the ovarian follicles become mature for ovulation (Montiel & Ahuja, 2005). PPI is regarded as one of the main causes of extended ICP (Blanc & Agabriel, 2008). PPI is influenced by a number of factors, such as prepartum feeding level as reflected by body condition at calving, postpartum nutritional status and parity of the cow (Sanz *et al*., 2004), suckling interval (Sanz *et al*., 2004; Montiel & Ahuja, 2005) cow-calving season due to nutritional factors (Sanz *et al*., 2004). Light and temperature (Short *et al*., 1990), dystocia (Sanz *et al*., 2004; Short *et al*., 1990), the presence of a bull (Short *et al*., 1990), breed and age of parity (Short *et al*., 1990; Cushman *et al*., 2007) and sire breed (Cushman *et al*., 2007) may also have an influence on PPI. Differences in PPI, as reflected in variances in ICP between breeds or progeny of different sires reflect a genetic base for PPI (J. v.d. Westhuizen. Personal Communication. SA Studbook. P.O. Box 270, Bloemfontein. 2012).

Although many factors affect postpartum anoestrus, nutrition and suckling are the major influences on the resumption of postpartum ovarian cycles. Nutrition and suckling affect hypothalamic, pituitary and ovarian activity and therefore inhibit follicular development. Under-nutrition contributes to prolonged postpartum anoestrus, particularly among cows dependent upon forage to meet their food requirements (Montiel & Ahuja, 2005). The nutritional status or balance of an animal is evaluated by means of the Body Condition Score (BCS) parameter. BCS reflects the body energy reserves available for metabolism, growth, lactation and activity. There is a relationship between energy balance and time to the resumption of postpartum ovarian activity. Inadequate nutrition results first of all in weight loss, then a decrease in the BCS and finally the cessation of the oestrous cycle. Suckling probably interferes with the hypothalamic release of GnRH and suppresses the release pulsatile LH which leads to an extended postpartum anoestrus (Montiel & Ahuja, 2005), although the exact interaction by which suckling extends post-partum anoestrus is uncertain (Pérez-Hernández *et al*., 2002). Other factors that influence the anoestrus period after calving and cause a longer ICP are: general infertility, uterine involution, short oestrus cycles and post partum anoestrus

(Short *et al*., 1990). A number of management practices have been suggested by Short *et al*. (1990) that could reduce PPI.

Although there are a number of limitations to the use of ICP as a measure of female reproductive performance, there is no current alternative to ICP as a measure of reproductive performance (Roughshed *et al*., 2005). The SANBRIS developed the RI to enable the comparison of animals with different AFC and ICP values and acts as a measurement of the overall reproductive performance of a cow. With the RI it is possible to compare cows with different AFCs and ICPs. The standard of comparison for the RI is the average reproduction performance of all cows (irrespective of breed) participating in the SANBRIS (Bergh, 2006).

2.3.3. Growth

The growth curve and mature size

The growth of an individual is determined, like other traits by additive gene action and genetic and non-genetic factors. These genetic combinations are influenced by, and interact with, environmental conditions such as climate, nutrition, and management, as well as intrinsic factors such as sex, age and physiological status. Other extrinsic factors like maternal effects and random environmental factors also play a role in the ultimate phenotypic expression of growth (Arango & Van Fleck, 2002).

Growth follows a sigmoid curve. The growth curve has a self-accelerating phase, followed by a linear phase and ends with a self-decelerating phase. The self-accelerating phase is a period in which cells double at regular intervals. This doubling rate does not last for a long time and is followed by a period of linear growth in which complex mechanisms are developed to acquire and transport nutrients to where they are is needed. Finally, the self-deceleration phase starts when the animal approaches its mature size. During this phase there is a genetic restraint on further growth, set in motion by hormonal signals (Lawrence & Fowler, 2002).

A number of other environmental factors also influence mature size (Fritzhugh *et al*., 1967). These include nutrition, management and climatic factors such as rainfall, temperature and temporary environmental effects (Fritzhugh *et al*., 1967). Mature cow weight not only reflects differences in size-associated skeletal size and lean growth, but also fatness (Arango *et al*., 2002). The genetic proportion of mature cow weight is mostly due to additive genetic variation (Fritzhugh *et al*., 1967). Some conflict exists in the literature exactly when cows reach mature weight. Morrow *et al*. (1978) defined average weight after four and a half years, Kaps *et al*. (1999) six and a half years, Mac Neil *et al*. (1984) seven years and Smith *et al*. (1976) six to nine years. It is clear that it is difficult to determine exactly when animals stops growing (Bullock *et al*., 1993). It would, however, appear if cows accumulate most of their final weights as four year olds and final height as three year olds (Arango *et al*., 2002).

Efficiency of growth

Efficiency of growth is usually expressed as a ratio between output/input where output is seen as live weight gain and input as energy consumed (Lawrence & Fowler, 2002). The biological efficiency of cattle depends upon the interaction between their genetic potential for efficiency and environmental factors such as the availability and variability of feed resources (Johnson *et al*., 2010). The utilisation of cattle with different genetic merit for production is therefore a logical response to environmental variation (Johnson *et al*., 2010). Cattle with high growth rates are associated with higher efficiency in energy utilisation (Cundiff *et al*., 1981). The improvements in feed efficiency are therefore largely due to increased growth rates and selection for lean growth (Webb & Casey, 2010). It has been suggested that there is less room for the improvement in feed utilisation than there is for improvement in the efficiency in maintenance functions (Pitchford, 2004). An analysis of the shape of the growth curve should indicate which areas should be targeted for improved efficiency (Menchaca *et al*., 2006).

Maternal component of growth

Growth traits like birth and weaning weight are determined by the calf's own additive genetic merit as well as the maternal component. These traits can be further separated in additive genetic and permanent environmental components (Deese & Koger, 1967; Van Niekerk *et al*., 2004). The maternal component mainly represents the dam's milk production and mothering ability, although the uterine environment and extra-chromosomal inheritance may also have an effect. The dam's genotype therefore has an effect on the phenotype of the young through a sample of half her direct, additive genes for growth as well as through her genotype for maternal effects on growth (Meyer, 1992).

It was postulated by Barker *et al*. (1993) that postnatal growth and physiology are influenced by stimulus experienced *in utero.* Maternal nutrition therefore potentially affects not only cow productivity but also post-weaning calf productivity (Larson *et al*., 2009). The majority of researchers have hypothesised that the effects of variation in nutrient intake would have greater effects in late pregnancy than in early pregnancy because the majority of foetal growth occurs in the later part of gestation (Funston *et al*., 2010). However, it was recently shown by Larson *et al*. (2009) that protein supplementation during late gestation, as well as increased global nutriënt supply throughout gestation, may increase calf birth weight.

Maternal weaning gain evaluations divide the weaning gain of the calf into a contribution from calf growth (direct weaning gain) and from maternal environment of the cow (maternal weaning gain). A major component of the maternal environment created by the dam is the nutrition the calf receives through milk (Clutter *et al*., 1987).There is a positive relationship between the breeding value for milk for the dam, actual milk production and the weaning weight of calves (Marston *et al*., 1982). Meyer *et al*., (1994) found a high (0.8) correlation between direct milk yield and maternal weaning gain. Milk production is therefore the main determinant of maternal effects on the growth of beef calves (Rutledge *et al*., 1971; Clutter *et al*., 1987; Meyer *et al*., 1994). Milk quantity rather than milk quality is reported to be more important in its influence on weaning weight (Rutledge *et al*., 1971).

The actual milk production of the dam is influenced by breed (Holloway *et al*., 1985; Jenkins & Ferrell, 1992; Brown & Brown, 2002), nutrition (Holloway *et al*., 1985; Jenkins & Ferrell, 1992), year (Rutledge *et al*., 1971), age and season of calving (Grings *et al*., 2007) as well as the calf's demand for milk and nursing frequency (Mezzadra *et al*., 1989). Suckling frequency is related to the milk production of the cow and the weight of the calf (Odde *et al*., 1985). There is a close relationship between milk intake and forage intake of nursing calves (Tedeschi & Fox, 2009). Calves of dams that have lower milk production are reliant on forage earlier in lactation, and to a greater extent, on alternative food sources of lower nutritional value than milk (Clutter *et al*., 1987; Tedeschi & Fox, 2009). Calf body weight and forage dry matter intake is correlated with calf milk intake (Tedeschi & Fox, 2009). Nursing calves become increasingly dependent on forage after 60 to 90 d of age to maintain adequate normal growth, depending on the quantity of milk intake (Tedeschi & Fox, 2009). The forage quality within a rangeland system can therefore affect growth rate of calves through influences on the milk yield of dams and quality of the forage portion of a calf's diet (Grings *et al*., 1996).

2.4. SELECTION FOR BEEF COW EFFICIENCY

2.4.1. Cow size

The body size or mature weight of a cow has an important effect on the way it responds to the climate, its food resources and other seasonal influences (Arango & Van Fleck, 2002). The cow's response to the environment is mainly due to the influence that the size, and therefore the relative surface area exposed to the environment of an animal, has on the heat exchange taking place between it and its environment (Hafez, 1968). Species that are adapted to cold climates have a digestive body type; i.e. large body size in relation to its surface area. A digestive body type has a relative smaller surface area that is exposed to the environment which effectively reduces heat loss. Species adapted to warm climates have a respiratory body type; i.e. highly vascularised skin and a large surface area to enable them to maximally dissipate excess heat (Hafez, 1968; Bonsma, 1983). The morphology of cattle that are adapted to cold climates would be a compact body with short neck and legs while cattle that are adapted to sub-tropical environments should have a rangy frame with long body extremities (Hafez, 1968).

A number of methods are used to determine cow size. The most popular methods are frame size and mature weight (Arango & Van Fleck., 2002; Vargas *et al*., 1999). Mature weight can be defined as the average weight at maturity independent of short-term fluctuations in size due to environmental effects of climate and food supply (Fitzhugh, 1976) on body condition (Klosterman *et al*., 1968). The SANBRIS records mature cow weight, body length and shoulder height as measures of body size (Vermaak, n.d). The first cow weight recorded after four years of age is used as mature weight (Vermaak, n.d).

According to Dickerson *et al*. (1974), the two most important components of efficiency in beef cows are mature weight and milk production. Kattnig *et al*. (1993) suggests that beef cow efficiency can be improved if cow size is tailored to the environment. The existence of an optimal cow size is often debated (Buttram & Willham, 1989; Arango & Van Fleck, 2002). It is postulated by some authors that optimum mature weight for efficiency differs among breeds and types (Brown *et al*., 1989; Johnson, *et al*., 1990). It is generally agreed that optimal cow size depends on the production system and environment (Morris & Wilton, 1976; Anderson, 1978; Dickerson, 1978; Fitzhugh, 1978). Research done in the 1970s by Dickerson (1970;1978) recommended that selection for optimal cow size should be aimed at those animals whose mature size is best adapted to the environment, breeding system and market factors of the area of production. Dickerson (1970; 1978) also suggested that selection should primarily be focused on the improvement of functional components of performance such as reproduction, relative growth and body composition.

Numerous authors have made suggestions on what mature size should be optimal for which environment. Bonsma (1983) suggested that large framed cattle should thrive in the semi-arid tropics, whilst smaller framed cattle should be best suited in the humid tropics. Dickerson (1978) stated that larger bodied cows have an advantage when there is an abundant food supply, and smaller framed cows are reportedly better adapted and therefore more efficient in hot and dry climates. Dickerson (1978) was supported by Solis *et al*. (1988) who suggest that cows with the potential to store and mobilise fat are more efficient within an environment with limited nutrients, whereas cows that have larger protein stores are more efficient when nutrients are not a limiting factor. Taylor (2006) suggests that smaller frame size should be considered when selecting for productive animals under extensive, hot and dry climatic conditions in Southern Africa.

Maintentenance cost is one of the most important factors that determine the biological efficiency of beef cattle (Arango & Van Fleck, 2002). An adult cow require more than 50% of her total energy intake for maintenance (Arango & Van Fleck, 2002). The maintenance cost of a cow should however be considered in light of Kleiber's theory, which states that metabolic weight = live weight ^ 0.75 (Kleiber, 1932). Kleiber's theory indicates that although a larger cow consumes more nutrients than a smaller cow the percentage additional nutrient requirement of larger cows is less than its additional weight as a percentage. A cow that weighs 545 kg weighs 20% more than a 454 kg cow, but her maintenance requirements are only 13% higher (Johnson *et al*., 2010).

It was previously shown that the majority of South Africa's rangeland is classified as either arid or semi-arid (Schulze, 1997) and that insufficient nutrient intake is the most important constraint on extensive cattle production in South Africa (De Waal, 1990). In a classic five year study conducted on nine breeds of cattle it was found by Jenkins & Ferrell (1994) that nutrient availability affected the ranking for breed mean efficiencies. Jenkins & Ferrell (1994) found that breeds with moderate genetic potential for growth and milk production were more efficient when nutrient availability was limited because of higher conception rates. These researchers found that breeds with the highest genetic potentials for growth and milk production were the most efficient at high levels of nutrient availability because feed availability was sufficient for the genetic potentials to be expressed. Jenkins & Ferrell (1994) therefore suggest that cow efficiency is maximised at a level of feed intake that does not limit reproduction and also provides sufficient energy for milk production to meet the growth potential of the breed as expressed in the calf. According to the conclusions of Jenkins & Ferrell (1994), and the prevailing environmental conditions of a large portion of the South African beef production environment, genotypes with moderate genetic potential for growth and milk production should theoretically be more efficient for South African conditions.

The significant influence of cow size on production efficiency is the reason why traits such as mature weight, height and length, are included in selection criteria (Arango & Van Fleck, 2002). Cow weight is frequently used by South African farmers to control mature size (Crook *et al*., 2010). In the late 1970s and

1980s there was an international trend to select for larger cattle (Buttram & Willham, 1989; Taylor, 2006). The result of selection for larger cattle would have been a net increase in growth rate, but it may have had a negative impact on female fertility traits (Vargas *et al*., 1999).

2.4.2. Adaptation

The recent emphasis on selection for growth has altered the rate and extent of the underlying physiological processes governing growth and development in livestock (Webb & Casey, 2010). Concerns have been raised about the negative influence of selection for growth may have had on the well-being, longevity, reproduction efficiency and susceptibility to stress and metabolic and infectious diseases of livestock (Green *et al*., 2007). The advantages posed by the lowered physiological stress of adapted animals are perceived as being important for efficient beef production (Prayaga *et al*., 2009) and could address the negative aspects of selection for growth. It was suggested by Frisch (1981) that selection response for growth in a stressful environment is not due to an improvement in the inherent genetic potential of the animal, but due to increased resistance to environmental stress. According to Nardone (1998), it is necessary to establish whether it is possible to select for high-producing cattle with heat tolerance. Nardone (1998) suggests that a measurable index of heat tolerance must be identified and the genetic correlation between heat tolerance and productive and reproductive traits estimated.

Rectal temperature is a good indication of core body temperature, while respiration rate can be used to measure the extent to which cattle make use of respiratory evaporation to decrease their body temperature (Bianca, 1968). Both indices are used to determine heat tolerance (Bernabuccil *et al*., 2010). In a review by Nardone (1998) it is reported that heritability estimates for rectal temperature ranged from 0.16 to 0.64. More recent estimates were reported as: 0.12 (Prayaga & Henshall, 2005), 0.18 (Burrow, 2001) and 0.21 (Prayaga *et al*., 2009).

A favourable genetic relationship between rectal temperatures and most weights and period weight gain (rg = - 0.20 to - 0.49) was reported by Burrow (2001). In the same study a low to moderate, favourable genetic relationship was found between rectal temperature and pregnancy rate (-0.16) and days to calving (0.16). Prayaga & Henshall (2005) found that there is a moderate negative genetic correlation between rectal temperature and growth traits, which may indicate that animals that have the ability to handle heat also have a genetic potential for growth. Prayaga *et al*. (2009) furthermore found a strong negative genetic correlation (–0.97) between steer beef yield and Brahman heifer rectal temperature, indicating a favourable genetic association. These researchers concluded that selection for productive and pubertal traits in tropical beef cattle genotypes would not adversely affect their tropical adaptability.

Morphological and anatomical characteristics partially explain differences in heat tolerance among species and breeds (Bonsma, 1983; Gaughan *et al*., 2009). One of these characteristics is a short glossy coat in cattle, which is controlled by the slick hair gene. Slick-haired cattle are better able to regulate body temperature than their wild-type contemporaries (Dikmen *et al*., 2008). In a controlled environment experiment it was found that when hair was clipped from the body of a long-haired cow, the difference in sweating rate between slick-haired and long-haired cows was eliminated (Dikmen *et al*., 2008). The heritability of sleek hair has been reported as 0.28 (Prayaga & Henshall, 2005) and 0.62 (Prayaga *et al*., 2009). Prayaga & Henshall (2005) found that the genetic correlation between coat score and growth traits were moderately negative, which indicates that as the animal's ability to regulate heat increase, so does growth at a genetic level.

Fitness

Fitness is described by Barker (2009) as the measure of the degree of the relationship between the trait and survival. Fitness is composed of several components such as "number of parities", "litter size" and "survival of progeny" (Beilharz *et al*., 1993). Fertility is therefore an important indicator of fitness. Fitness is influenced by a number of components that are in turn influenced by the environment (Beilharz *et al*., 1993). The components of fitness are influenced by a large number of genes that influence how an animals will perform in terms of fertility in a given environment. The fitness concept is in accordance with the Darwinian concept of survival of the fittest (Darwin, 1859). According to Van Niekerk & Neser (2011) fitness implies that the population with the highest gene frequency for adaptability within a given environment will have the highest reproduction rate and that there are interactions between the animal and its physical environment.

The components of fitness require resources for functioning (Beilharz *et al*., 1993). The resources that are the most important in farm animal production are energy, nutrients and time (Glazer, 2009). Beilharz *et al.* (1993) developed the the resource allocation theory that argues that the environmental resources available for a population of animals that was selected in a specific environment are optimally distributed between production and reproduction. The distribution of resources is due to the continuous selection for higher reproductive values in the natural environment. The theory therefore implies that all natural populations are limited in their fitness by the environmental resources that are available in their respective niches. Thus, any additional selection for increased performance in a production-related trait would lead to declines in reproduction, unless there is a concurrent increase in resources (Mignon-Grasteau *et al*., 2005). The available environmental resources therefore determine the phenotype that can be sustained most efficiently, and the genotypes that are selected for on the basis of such phenotypes (Beilharz *et al*., 1993).

Different genotypes have different demands on the environmental resources for the full expression of their potential (Beilharz & Nitter, 1998). A genotype's resource-demanding processes will not be able to be expressed in its full potential in environments with fewer resources available than that is required, thus causing those animals with high genetic potential to have lower performance levels than animals that have less genetic potential, but whose lower potential is fully supported by the resources in the specific environment (Beilharz & Nitter, 1998 & Notter, 1998). The result of such interactions is a typical genotype x environment (G x E) interaction (Rauw, 2009).

G x E interactions

G x E interactions constitutes the basis of the adaptation of a species to its environment (James, 2009). G x E interactions are manifested when similar genotypes show a different phenotypic response across one or more environments (Beffa, 2005). The different responses are due to different genes that are expressed for the same genotypical trait in different environments (Bertrand *et al*., 1987). James (2009) described various types of environmental interactions. Much of the importance of G x E interactions in livestock stems from the problem of making genetic improvement in a population with significant G x E interactions. James (1961) suggests that genetic progress can be made when there is significant G x E interactions by doing selection in one environment or selection for two strains in two different environments or doing selection based on an index combining performance in both environments.

G x E interactions in South African Bonsmara herds were investigated by Neser *et al*. (1996), Neser *et al*. (1998) Nephawe *et al*. (1999), Neser *et al*. (2008) all of whom found G x E interactions. By implication it can be argued that certain genotypes within the Bonsmara breed are better adapted and more productive in specific environments. If, according to the recommendations made by James (1961), adapted genotypes were selected for within specific environments, these genotypes should also perform better in similar environments. The possibility of a G x E interaction is, however, provided for by the inclusion of a Sire x Herd interaction (as an additional random effect) in the prediction of Best Linear Unbiased Prediction (BLUP) breeding values for the Bonsmara breed (J. v.d. Westhuizen. Personal Communication. SA Studbook. P.O. Box 270, Bloemfontein. 2011).

2.4.3. Reproduction

Selection for both male and female fertility is desirable due to the variability in the traits (Meyer *et al*., 1990). Although it is generally accepted that it is necessary to maximise the reproductive potential of beef cattle, Lishman *et al*. (1984) argue that it would be beneficial to optimise rather than maximise reproduction because the gross margin per cow increases parallel with the calving rate, but the margin per cow does not necessarily show the same response.

Relatively few heritability estimates have been reported for fertility in beef cattle, although it is evident from these reports that fertility traits are heritable (Rust & Groeneveld, 2001; Cammack *et al*., 2009). In a review of fertility traits Cammack *et al*. (2009) found that heritability estimates for fertility ranged from ≤ 0.10 to ≥ 0.60. The heritability of reproductive traits in the Bonsmara is presented in Table 2.3.

Table 2.3 Heritability of Bonsmara fertility traits (Van der Westhuizen *et al*., 2011)

Trait	AFC	ICP1	ICP2	ICP3
h^2	0.23	0.08	0.11	0.1

There are also important genetic correlations between reproductive traits and other production traits that are moderate to highly heritable (Cammack *et al*., 2009). It is for that reason important that measures of reproductive efficiency are included in the breeding objective of beef breeders (Cammack *et al*., 2009; Meyer *et al*., 1990). Genetic improvement for fertility is unfortunately hampered by a lack of information, low heritability and the delayed expression of the trait (Prayaga, 2004; Cammack *et al*, 2009).

The heritabilities of fertility traits are difficult to estimate because the expression of the reproductive potential is often constrained by management systems (Notter & Johnson, 1988; Meyer *et al*., 1990; Rust & Groeneveld, 2002). Moreover, the underlying genetic merit for fertility is often not expressed, due to the threshold nature of fertility traits. There are only two outcomes possible for successful reproduction: whether the cow is pregnant or not. Degrees of pregnancy are not observable. The environment has a strong influence on which side of the threshold trait an individual falls (Martin *et al*., 1992). According to Prayaga (2004) and Rust & Groeneveld (2002), the general consideration is that selection has a limited potential to improve fertility in beef cattle.

According to Martin *et al.* (1992) there are two approaches to follow when selecting for improved fertility. The *direct* approach involves the physical selection for fertility traits. This should include traits such as scrotal circumference, age at puberty, AFC as well as calving date and the proportion of heifers in production at a given age. Martin *et al.* (1992) suggest that the use of any prospective fertility trait will depend on the ease of measurement and the inherent relationship with fertility. The second or *indirect* method these researchers proposed is to use an array of traits that have an indirect effect on fertility. Traits to be considered are milk production, growth rate, calving ease, and body condition. Selection for optimum combinations of these traits should create a favourable "genetic environment" for fertility. The researchers suggest that using this method will set the levels of production traits in such a way that expressed fertility is optimised (Martin *et al*., 1992).

2.4.4. Growth

Growth is highly heritable, with heritabilities ranging from 0.24 to 0.61 (Koots *et al*., 1994) and fast genetic progress is possible when animals are selected for growth rate (Lawrence & Fowler, 2002). The heritability of growth and size traits in the Bonsmara is presented in Table 2.4 (Van der Westhuizen *et al*., 2011).

Table 2.4 Heritability of Bonsmara growth traits (Van der Westhuizen *et al*., 2011)

Trait	Birth direct	Wean direct	Year direct	18 Month direct	Mature weight	Birth maternal	Wean maternal
h^2	0.39	0.22	0.27	0.29	0.32	0.08	0.12

Selection for growth is complex, since traits like birth and weaning weight are determined by the animal's own additive genetic merit as well as the maternal component, which can be further separated in an additive genetic and a permanent environmental component (Van Niekerk *et al*., 2004). It is well known that selection for a higher growth rate will eventually increase the mature size of animals if it is not contained (Morris & Wilton, 1976). The increase in mature size is due to the positive correlation between weights at different ages (Prayaga & Henshall, 2005). There is also a negative correlation between mature size and age of maturation (Brody, 1945). Selection for size will therefore increase the time taken to reach maturity (Fitzhugh, 1976). The shape of the growth curve is largely determined by the relationship between size and the rate of maturation (Taylor & Fitzhugh, 1971).

According to Fitzhugh (1976) and Mostert *et al.* (1994) there are several reasons for wanting to change the shape of the growth curve. These authors argue that the alteration of the growth curve will resolve the genetic antagonism between rapid, efficient early growth of slaughter animals and the desired small size of parental stock (Dickerson *et al*., 1974). Changing the growth curve will improve the intrinsic physiological efficiency through increased maturation rate (Taylor & Young, 1966). An altered growth curve should reduce dystocia by decreasing birth weight of the calf relative to the dam's size (Monteiro, 1969). A changed growth curve should also achieve a younger AFC by decreasing the time to sexual maturity or to decreasing carcass fat content at preferred market weights by increasing time to chemical maturity (Fitzhugh, 1976).

Genetic change in the shape of the growth curve is limited by the degree of genetic flexibility in the shape of the curve. The genetic flexibility depends upon the degree of interdependence of the size, rate and inflection of the parameters (Fitzhugh, 1976). Although theoretically possible, the basic shape of the sigmoid growth curve as well as the sequence of physiological events remains virtually unchanged (Webb & Casey, 2005). The rate of these processes has, however, increased remarkably (Webb & Casey, 2010).

Scholtz *et al*. (1990) conducted a meta-study on the results of selection experiments on rats and poultry. Scholtz (1990) concluded that selection for increased body weight or growth rate may have an adverse effect on body composition, fertility and survival rate. These authors suggested that selection should rather be focused on increased feed efficiency because it may lead to fewer adverse effects. Webb & Casey (2010) also postulated that selection for growth and efficiency may have reached the physiological limits of animals to cope with the demands of maintenance, accelerated growth, development, adaptation and reproduction.

Growth rate and puberty

Heifers reach puberty at the onset of their first oestrus that is followed by a normal luteaal phase (Moran *et al*. 1989). Factors such as weight, size, plane of nutrition, breed, season and social environment have an influence on the age at which heifers reach puberty (Moran *et al*. 1989). First ovulation is, however, not synonymous with puberty in most heifers. Some heifers may in fact be quite incapable of reproducing until well after their first ovulation (Moran *et al*., 1989). It has been suggested that the age at which puberty is reached is the best measure of fertility (Martin *et al*., 1992) and that a younger AFC will increase the number of calves born for a given number of animals (Rust & Groeneveld, 2001). Although there is a need to reduce the age of puberty, there are certain problems associated with precociousness such as a greater incidence of dystocia (Lawrence & Fowler, 2002). Heifers that calve while they have inadequate body size have a greater propensity for dystocia than larger heifers (Wehrman *et al*., 1996). It is important to differentiate between puberty and sexual maturity. The latter only occurs when an animal is able to express its full reproductive potential (Lawrence & Fowler, 2002).

Martin *et al*. (1992) found that breeds that gain weight faster and reach a larger mature size also reach puberty at a later chronological age than those breeds with a slower weight gain and with smaller mature size. The heifer offspring of sires from breeds with a large mature size tend to be older and heavier at puberty than do heifers sired by breeds with smaller mature size (Martin *et al*., 1992). Breeds selected for milk production seem to reach puberty earlier than breeds selected for beef production (Martin *et al*., 1992). According to Hafez & Hafez (2008), it is apparent that puberty occurs at a specific physiological rather than a particular chronological age. It is the interplay between hormones and the subsequent interaction of the hormones on the target tissues that determine the onset of puberty. Puberty begins when the suppressive effects of estradiol on the hypothalamic-hypothyseal axis are overcome. This causes the first surge of gonadotropin secreted by the hypothalamus (Lawrence & Fowler, 2002). The gonadotropin in turn induces the gradual start of oestrogen secretion from the graafian follicle. LH and FSH from the pituitary gland are secreted at the same time. The increase the frequency of LH-peaks is followed by a pre-ovulary surge of LH (Hafez *et al*., 2008).

It is very difficult to distinguish between the effects of growth rate and those of the relationship between growth rate, age and live weight at puberty (Lawrence & Fowler, 2002). The same authors postulate that there is a physiological mechanism that can change the sensitivity of the hypothalamus to estradiol, but how this mechanism is triggered by growth rate, live weight and/or age remains uncertain. They also suggest that different factors may act as a trigger mechanism in the establishment of positive feedback on the hypothalamus. Heifers with a faster growth rate tend to reach puberty at younger ages than slower growing heifers. The differences in body composition between early- and late maturing breeds at similar live weights suggest that critical body fat or protein proportions can be the trigger to induce puberty (Lawrence & Fowler, 2002).

Growth rate and reproduction

Information on the effects of selection for body weight or growth rate on reproductive fitness in cattle is unfortunately limited (Scholtz *et al.*, 1990). A few assumptions regarding selection for growth and its influence on the reproductive efficiency of a cattle population can, however, be made. In his fundamental theorem of natural selection Fisher (1930) implied that reproductive fitness and body weight will be near the peak of fitness in a natural population. However, when selection for growth takes place, the population is no longer in a natural equilibrium. According to Falconer & King, (1953), reproductive fitness could be expected to decline when the mean of a population is moved in either direction due to selection pressure. The antagonistic relationship between fertility and milk production in dairy cows (Janson & Andreasson, 1981; Roxstrom *et al*., 2001) and the resource allocation theory of Beilharz *et al*. (1993) seem to support this theory.

The consequences of selection for growth, size and efficiency in production animals was reviewed by Scholtz *et al*. (1990), who concluded that selection for increased growth rate might have an adverse effect on fertility. There is therefore a concern that selection for a high growth rate might have negative effects on the fertility of cows (Barlow, 1978; Roux & Scholtz, 1984). However, contrasting results have been published by Burrow *et al*. (1991). Burrow *et al*. (1991) reported that cows with a high pre-weaning growth reared more calves over their lifetime, had lower numbers of calf mortalities and also calved earlier than cows with lower pre-weaning growth. Archer *et al*. (1998) found that the reproductive performance of Angus females selected for a high growth rate was similar to those of females where there was no deliberate selection pressure at all. Archer *et al*. (1998) also found that females selected for lower growth rates had a significantly poorer reproductive performance than unselected females. Burrow & Prayaga (2004) also found no changes in any of the female fertility traits in any of the lines selected for growth or low rectal temperatures in a selection experiment done on composite cattle. Unfortunately, only Burrow *et al*. (1991) examined the effects of selection on cow fertility throughout her entire lifespan.

Based on conclusions drawn from experiments done on rats and poultry, Scholtz *et al*. (1990) indicated that selection for body weight or growth rate might adversely affect the reproductive performance and body composition of cattle. The EBV trends shown in Figures 1.3 and 1.4 for Bonsmara growth and reproduction traits also seem to indicate that there is a negative relationship between growth and reproduction. Numerous studies, however, do not support this hypothesis (Burrow *et al*., 1991; Burrow & Prayaga, 2004; Archer *et al*., 1998).

2.5. CONCLUSION

It has been shown that large parts of the South African beef production region are not ideal for beef production. The majority of South African beef are therefore produced in extensive systems under environmentally challenging conditions. A number of environmental characteristics have been identified that could have an influence on the efficiency of beef production. It has also been shown that the well being and production efficiency of livestock in such challenging environments is dependent on the physiology of the animal to maintain its internal environment or *homeostasis*. The adaptive ability of cattle therefore plays an important role in the efficient production of beef in South Africa. The literature indicates that the mature size of a cow has an important influence on her maintenance requirement and her response to the environment. Cow size should therefore have an important influence on the adaptive ability of a cow. The optimisation of cow size should have the potential to improve the adaptive ability of beef cows and the efficiency of beef production in challenging environments. The characterisation of the influence of specific environmental factors on beef cow efficiency should also improve the understanding of the relationship between the beef cow and her production environment.

CHAPTER 3
MATERIALS AND METHODS

3.1. INTRODUCTION

The purpose of this study was to investigate the influence of the production environment on the production efficiency of Bonsmara cows in South Africa. To reach this aim a novel approach was followed. A dataset that contains the historical performance of Bonsmara cows as well as the prevailing environmental conditions to which animal were exposed to during their lifecycle were created. The geographic locations of specific Bonsmara breeders were established and the prevailing environmental conditions and the production region in which these breeders are located were determined by GIS tools. The environmental and production region classification information was obtained by GIS analysis from spatially referenced maps. The environmental characteristics and production region of each breeder's location were then linked to the particular Bonsmara cows that completed their lifecycle in that environment. The dataset was then statistically analysed to determine the relationship between Bonsmara cows and their environment.

3.2. MATERIALS

3.2.1. Bonsmara production records

South African National Beef Recording and Improvement Scheme

The SANBRIS are managed by the Animal Production Institute of the Agricultural Research Council (ARC) on behalf of the Department of Agriculture, Forestry and Fisheries (DAFF). The purpose of the SANBRIS is to supply the beef industry with objective performance information in order to improve the biological and economic efficiency of beef production through genetic improvement and improved management practices (Bergh, 2010). The SANBRIS publishes EBVs derived by BLUP for most participating breeds.

The SANBRIS records on-farm information regarding the birth information, mating data, pregnancy diagnosis, body condition scoring, pre-wean and weaning weight, cow weight calving and wean, 12- and 18-months weights, real time ultrasound scans and tick counts. Breeds that take part in the scheme also performs centralised performance and on-farm growth tests, where certain post-wean growth traits, feed conversion, body ratio measurements and carcass information of young bulls are measured (Bergh, 2010).

Study dataset

The June 2010 BLUP evaluation file were obtained from the SANBRIS for use in this study. The file contained pedigree and production records for 1 468 502 Bonsmara cattle collected since 1949. The production and reproduction measurements and EBVs that was recorded and calculated by the SANBRIS for each individual animal were included in the file. The file was subsequently merged with the production-region classifications and environmental characteristics of the Bonsmara breeders.

3.2.2. Vegetation classification systems

A number of vegetation maps describing the flora of South Africa have been published. The best known of these is the classic study of Acocks published in 1953 and updated in 1988 (Acocks, 1988). This was followed up by the classification system published by Low & Rebelo (1996). The latest research was published by Mucina & Rutherford (2006) and is called "VEGMAP". A discussion of the different vegetation classification systems is presented in Chapter 4.

3.2.3. Environmental characteristics

AGIS

The natural resource data used for this study were obtained from AGIS. The Agricultural Geo-referenced Information System (AGIS) is a spatial information system, co-managed by the DAFF and the ARC. It is a web-based system focused mainly on the provision of spatial data for natural resource information (A. Collett. Personal Communication. DAFF. Cnr Annie Botha and Union Street, Riviera, Pretoria. 2010). Most data sets are only available on a scale of 1:250 000. It is important to note that it was stressed by Collett (2008b) that the 1:250 000 scale maps of AGIS have limitations for use at farm level and that the scale can therefore lead to misinterpretation.

Rainfall according to AGIS

Data from ARC and South African Weather Service (SAWS) weather stations with a recording period of 10 years and more were used to compile the map. Surface trends were created from the monthly rainfall data. Regression analysis was then used to relate the difference between station rainfall values and trend surface values for specific months, to topographic indices such as rain shadows and aspect. These relationships and the trends surface were then used to model the rainfall surface from spatial topographic indices (AGIS., 2010). The South African annual rainfall according to AGIS is shown in Figure 3.1.

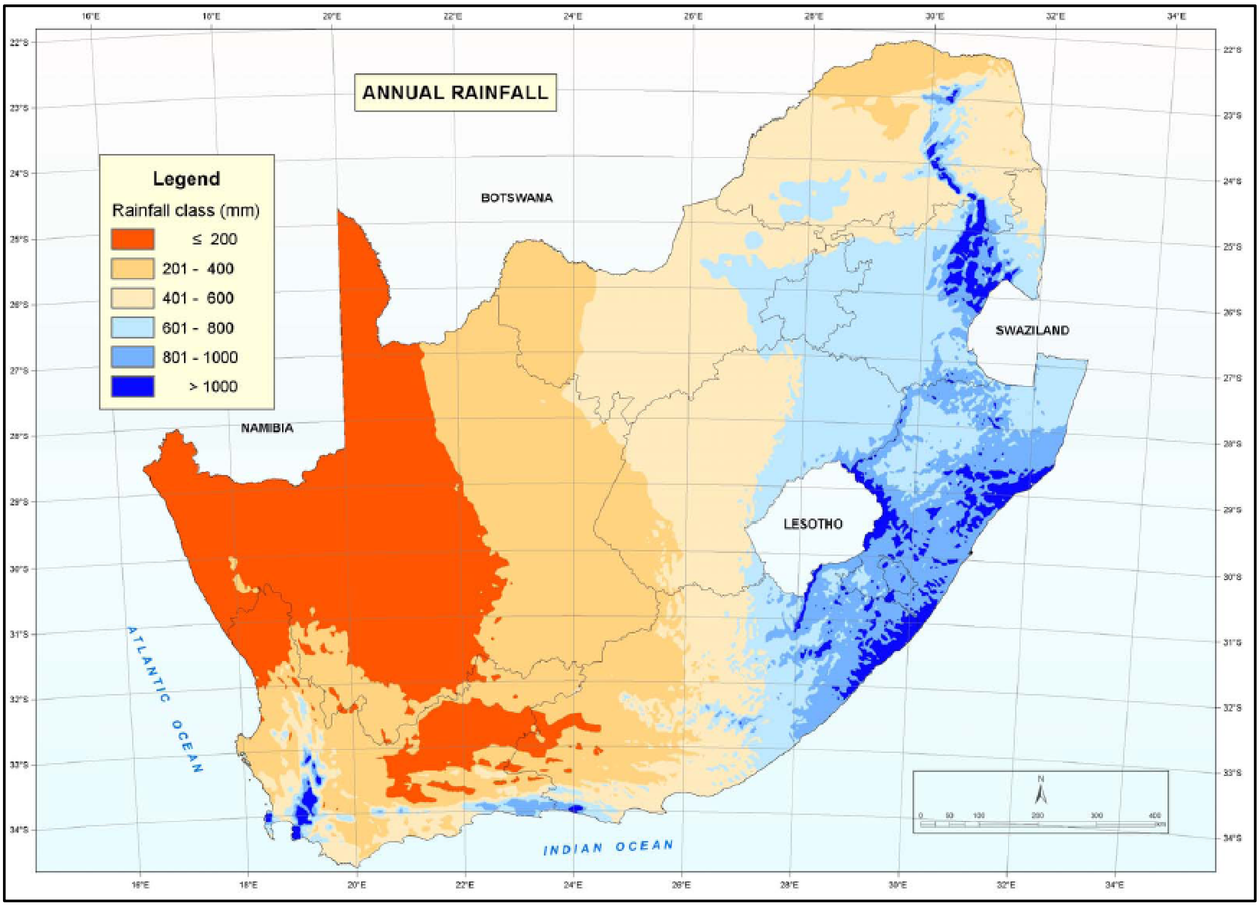

Figure 3.1 South African annual rainfall according to AGIS

Temperature according to AGIS

Temperature data from ARC and SAWS weather stations with a temperature-recording period of ten years or more were used to compile this map. For this map, long-term maximum temperatures were averaged for the warmest ten-day period of the year. Available temperatures were used by regression analysis to relate temperature data averaged per ten-day periods to topographic indices such as altitude, aspect, slope and distance from the sea. These relationships were then used to model a temperature surface from spatial topographic indices (AGIS., 2010). The South African maximum annual temperature according to AGIS is shown in Figure 3.2.

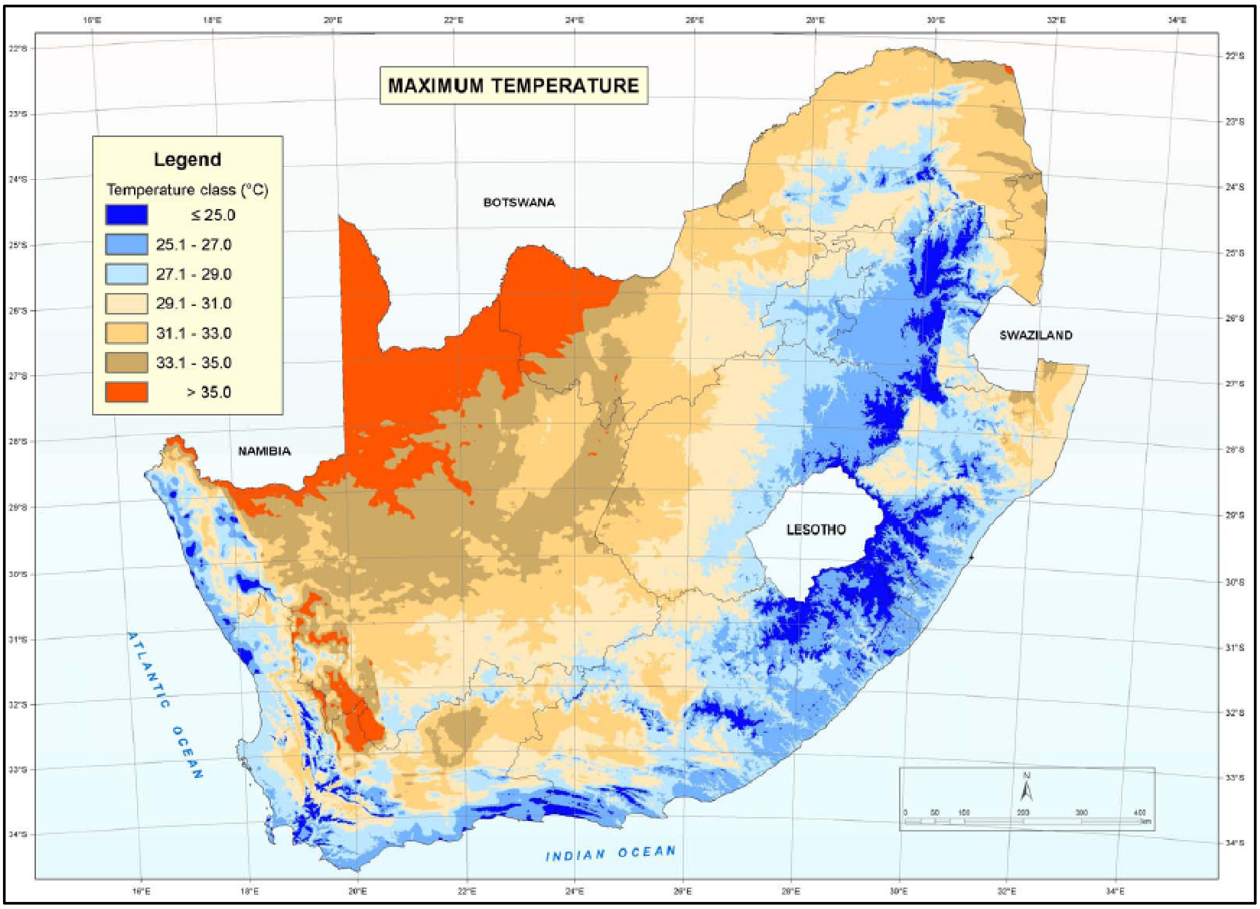

Figure 3.2 South African maximal annual temperature according to AGIS

Soil pH according to AGIS

The data for the map extracted from the National Soil Profile Database, 3 130 topsoil pH (H_2O) values were interpolated to construct the map. The map depicts areas of naturally occurring low-pH soils. The distribution of these soils is determined by present and past rainfall conditions, age of the landscape and soils, and the base status of parent materials. The source data are predominantly from uncultivated land and thus do not show the aggravating effect of secondary acidification on the soil's pH status (AGIS., 2010). The South African natural soil pH according to AGIS is shown in Figure 3.3.

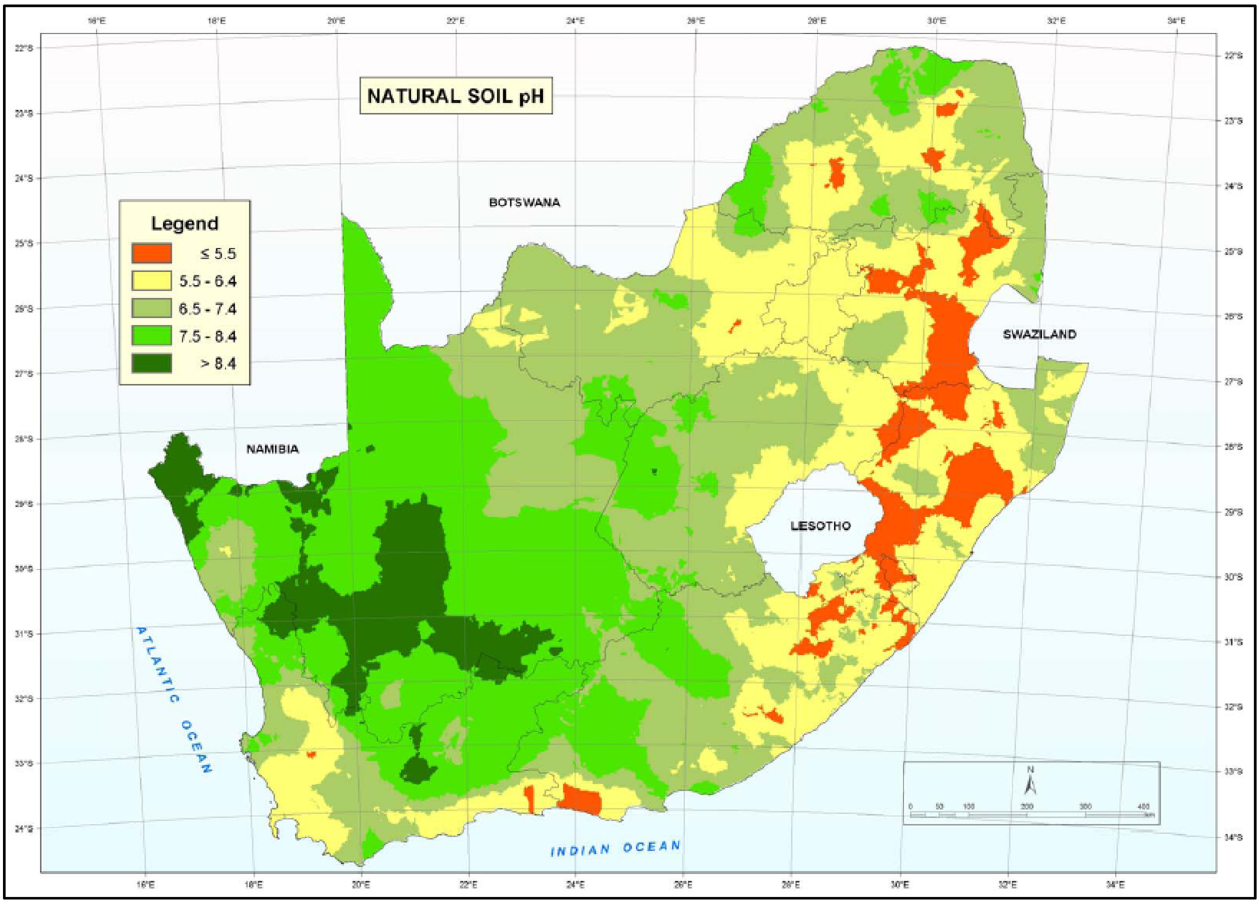

Figure 3.3 South African natural soil pH according to AGIS

CEC according to AGIS

The data for the map were extracted from the land type survey database. Values from 3 655 topsoil samples were interpolated. Land use that was linked to cultivation of any kind was excluded. Land use include agronomic cash crops, disturbed land, cultivated flowers, fruit trees, cultivated pastures, plantations, unknown cultivation, vegetables and vineyards (AGIS., 2010). The South African CEC according to AGIS is shown in Figure 3.4.

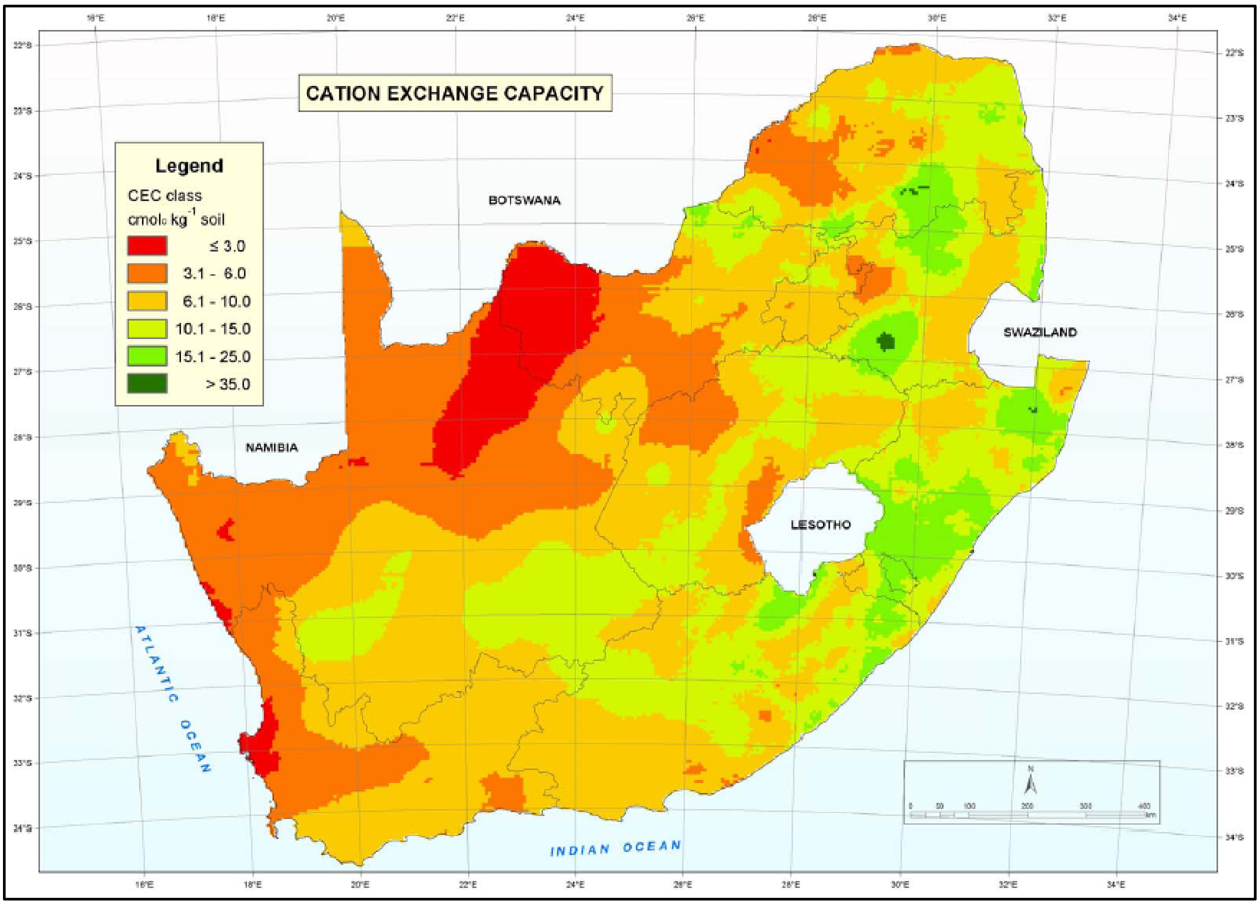

Figure 3.4 South African CEC according to AGIS

Soil organic carbon according to AGIS

The data for the map were extracted from the land type survey database. Values from 3 634 topsoil samples were interpolated. Land-use that was linked to cultivation of any kind was excluded. Land use include agronomic cash crops, disturbed land, cultivated flowers, fruit trees, cultivated pastures, plantations, unknown cultivation, vegetables and vineyards (AGIS., 2010).

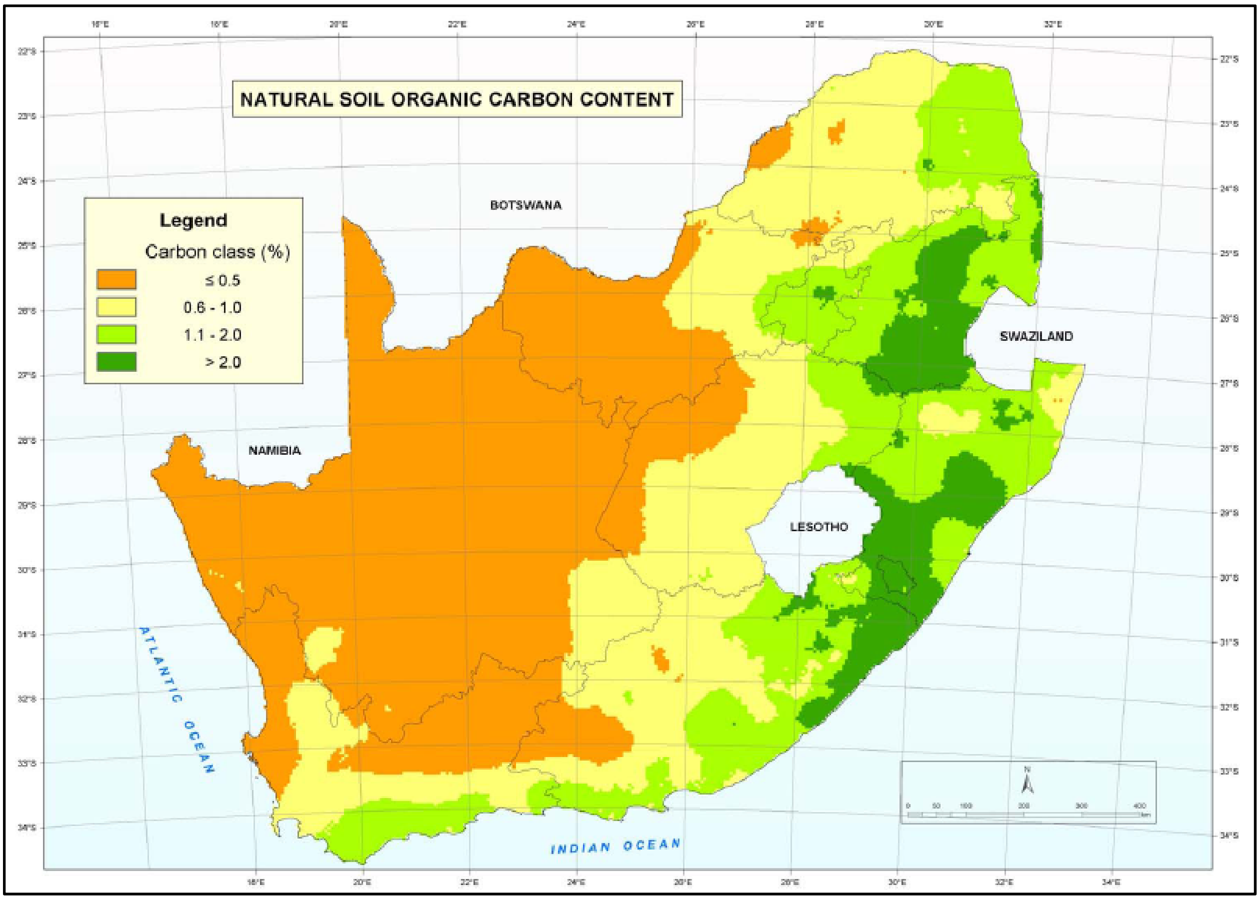

Figure 3.5 South African natural soil organic carbon content according to AGIS

Soil P according to AGIS

The data for the P map was extracted from the land type survey database. Values from 2 890 topsoil samples were interpolated. Land use that was linked to cultivation of any kind was excluded from the analysis. Land use include agronomic cash crops, disturbed land, cultivated flowers, fruit trees, cultivated pastures, plantations, unknown cultivation, vegetables and vineyards (AGIS., 2010).

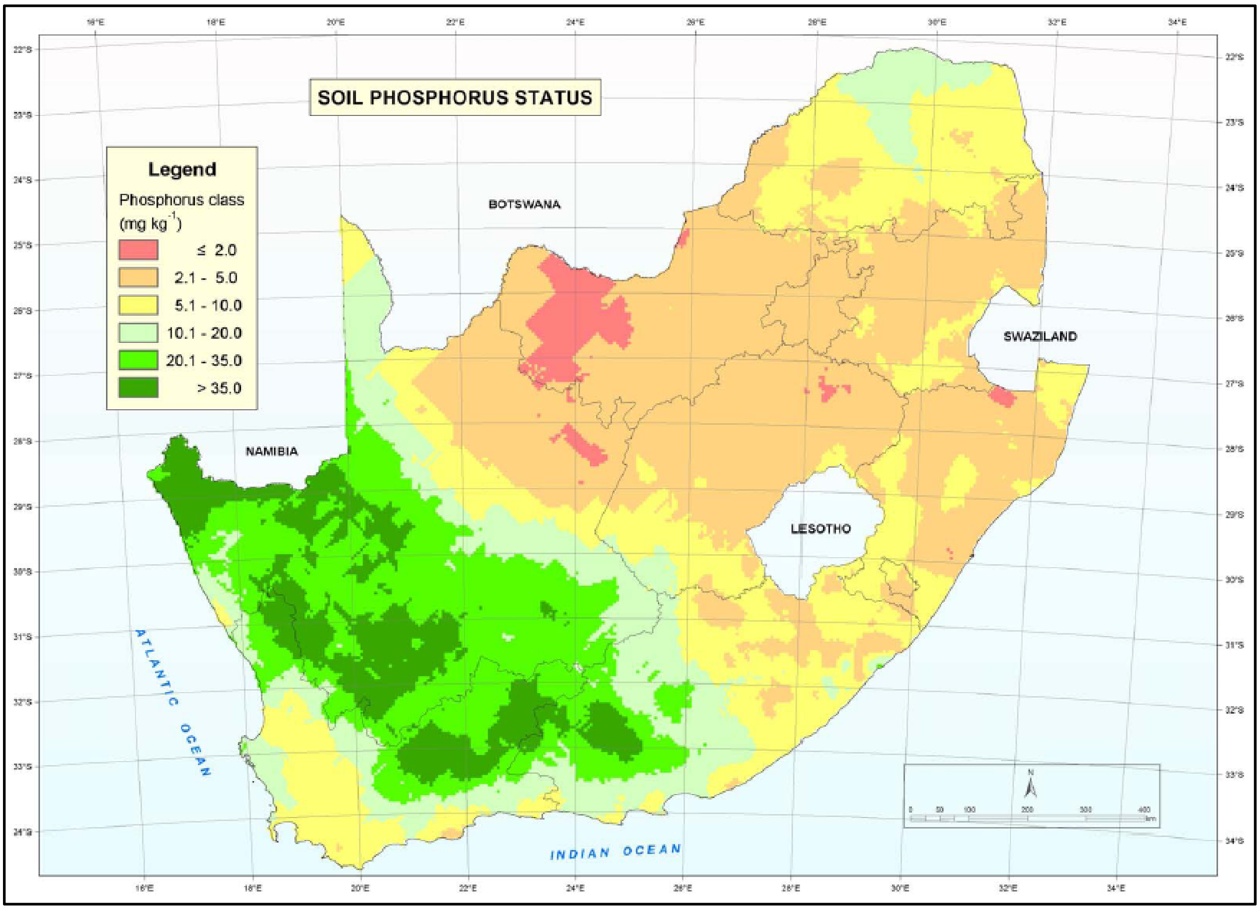

Figure 3.6 South African soil P status according to AGIS

Grazing capacity according to AGIS

The gc0106 grazing capacity layer is the latest (2010) unofficial grazing capacity map compiled by the DAFF. The map was produced by correlating the maximum normalised difference vegetation index (NDVI) image with animal unit (AU) values from earlier (1993) grazing capacity maps. Land cover and tree density were incorporated. Where overlapping occurred with transformed rangeland, the grazing capacity values were masked with land cover classes (AGIS., 2010). This grazing capacity map was compiled by means of remote sensing technology and is not as accurate as desired (P. Avenant. Personal Communication. DAFF. Cnr Annie Botha and Union Street, Riviera, Pretoria. 2010).

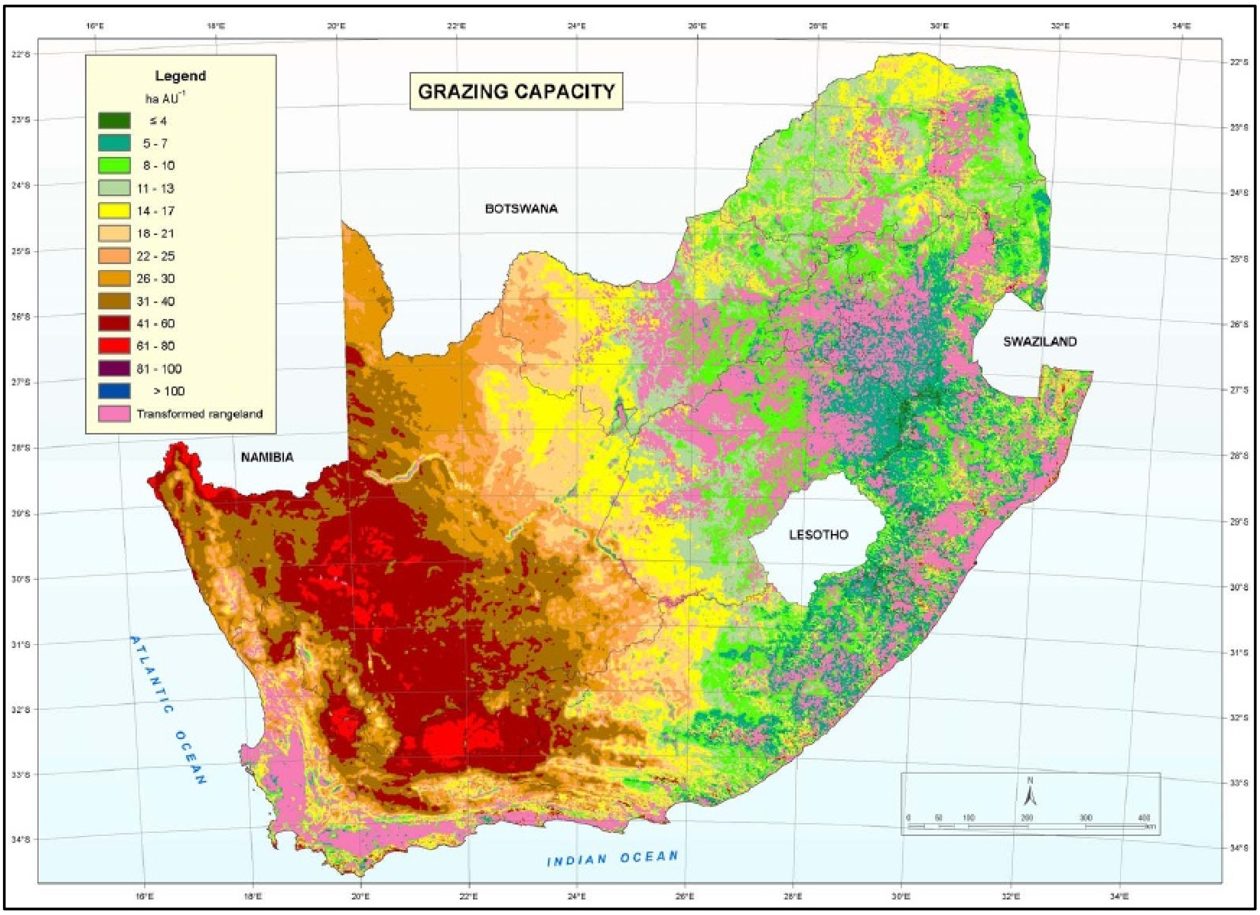

Figure 3.7 The grazing capacity of South Africa according to the gc106 layer

3.3. METHODS

3.3.1. Bonsmara breeder locations

The locations of the Bonsmara breeders were established first. The 423 active Bonsmara stud breeders were contacted and requested to supply the GPS waypoints of their herd locations. The farm locations of breeders who did not respond to the emails were determined by GIS tools. To find the locations of unresponsive breeders' farms, a SANBRIS database containing the farm name and closest town of each breeder was used. A GIS software program "Maptitude 4.5" and a farm portions layer supplied by AFRIGIS was used to locate each farm and determine its coordinates. The geographic locations of the breeders are presented in Figure 3.8. If there was uncertainty, the specific breeders were contacted telephonically to confirm their locations. The information on breeders who indicated that they had cattle registered under the same breeder number in different environmental regions was not included. The information of retired breeders, who had a significant amount of records on the final database, was included in the database.

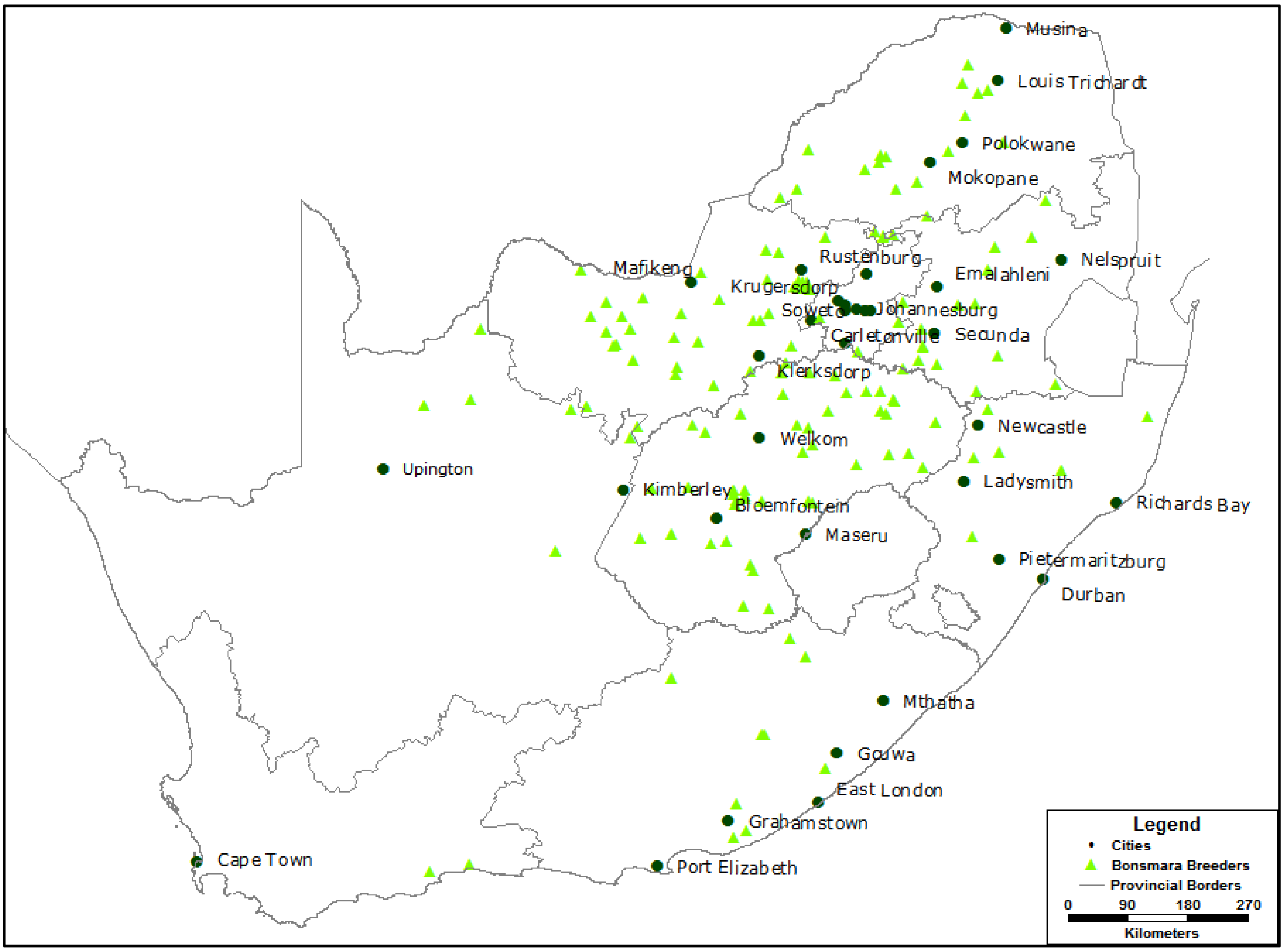

Figure 3.8 Locations of Bonsmara breeders in South Africa

3.3.2. Spatial analysis

Spatial information and decision support systems are an effective way of managing natural resource information (Hodson & White, 2010). A GIS is a computer-based system capable of capturing, storing, analysing, and displaying geographically referenced information (Anon, 2007). GIS interprets spatial information by layering the different data sets in order to reach overall conclusions (Collett, 2008b). Despite its many potential applications and innovative advances in software usability GIS is still only used by a fraction of potential users in agriculture (Hodson & White, 2010). The environmental data used in this study was available in the form of geo-referenced maps and a GIS analysis was used to layer and extract the relevant information from the different data layers.

Dataset construction

The data components were linked by means of a basic GIS analysis. GIS was used to link the location of the breeders with the prevailing environmental characteristics for that location. This was done by plotting the localities (GPS coordinates) of the Bonsmara breeders in a spatial environment with ARC-GIS 9.3 software. The environmental data characteristics (temperature, rainfall, CEC, soil pH, soil organic carbon, soil P and grazing capacity) data layers that were obtained from AGIS were then layered in the same spatial environment. The vegetation classification layers (Acocks, 1988 & Low & Rebelo, 1996 and VEGMAP, 2006) were then added to the spatial environment. The environmental characteristics and vegetation classification type for each location were then obtained by drilling through the layers of data. These characteristics were captured in a new dataset showing the environmental characteristics for each location (Breeder). This environmental property dataset was then merged with SAS 9.2® software with the June 2010 BLUP run file that contain the Bonsmara production records. The environmental and production datasets were merged on the breeder/location field. The combined dataset therefore included each animal's production records as well as the environmental characteristics to which they were exposed and the vegetation types associated with the locations.

3.3.3. Data processing

Derivation of environmental values

The EBVs that are published by the SANBRIS are derived by mixed model breeding values that remove the environmental influence in order to predict the additive genetic merit of the animal (J. v.d. Westhuizen. Personal Communication. SA Studbook. P.O. Box 270, Bloemfontein. 2011). The focus of this study is on the environment (E) component rather than the phenotypic (P) or genotypic (G) values.

The method followed to derive E values is as follows: The phenotype (P) of an animal is the result of its G inherited from its parents and the environment influence. It is mathematically described as:

$$P = G + E$$

The genotype (G) is the sum of the additive and non-additive genetic components, while E consists of both the known and unknown environmental effects (Falconer & Mackay, 1996). E is therefore simply calculated as E = P – G. For example, a cow with a mature weight (MW) P value of 505 kg and EBV (G) of + 5.5 kg will have a MW_E value of 499.5 kg. Thus the environment contribution to MW is 449.5 kg and the genetic component 5.5 kg, with the result of an animal weighing 505 kg. By concentrating on the environmental influence, free from genetic merit, the possibility of bias caused by differences in genetic levels in individual herds and regions is accounted for in this study. The environmental component abbreviations are presented in Table 3.1.

It could be argued that such a derivation of E values is not valid due to the possible influence of G x E interaction. As shown in the literature G x E interactions were found in the South African Bonsmara population (Neser *et al*., 1996; Neser *et al*., 1998; Nephawe *et al*. 1999; Neser *et al*. 2008). However, the current breeding value prediction models provide for the inclusion of sire x herd as an additional random effect to provide for the possibility of a G x E interaction (J. v.d. Westhuizen. Personal Communication. SA Studbook. P.O. Box 270, Bloemfontein. 2011).

Table 3.1 Environmental component abbreviations

Abbreviation	Explanation
BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period

Data editing

The June 2010 BLUP file obtained from SANBRIS contained a total of 1 468 502 Bonsmara records. The data were edited prior to the statistical analysis to remove the unwanted data from the dataset as described in Table 3.2.

Table 3.2 Number of records retained after each step of data editing

Criteria for record removal	Records
Retain only records of female animals with a MW measurement	65755
Link animal records with breeder location and environmental data	
Remove records without breeder location	27704
Remove records of breeders not located in the Dry Highveld Grassland-, Mesic Highveld-, Central Bushveld- and Eastern Kalahari Bushveld bioregions	23876
Compute E component and add to database	
Calculate average ICP for those cows that had more than 4 calves ((ICP1 +ICP2 +ICP3 /3))	
Retain animals with same owner from birth- to mature weight	17810
Remove animals that fall outside Bonsmara minimum breed standards for reproduction (AFC of > 0 and < 1170; ICP < 790)	17651
Calculate RI and remove cows with more than 15 calves (embrio donors)	17583
Remove records from breeders located outside the study region	16782
Retain only records of animals born from 1990	13853

3.3. STATISTICAL ANALYSIS

A statistical analysis of the 13 853 records that remained after the data editing was done by using the general linear method (GLM) of SAS® version 9.2 under MS/WINDOWS XP Professional (SP3).

Biological improbable records were removed from the dataset for accuracy’s sake prior to the statistical analysis. A total of 172 records (1.2% of the original data) were judged biologically improbable and removed. All records from breeders that had fewer than 50 animal’s records were finally removed. Data removal is explained in Table 3.3.

Table 3.3 Removal of biological improbable records for MW_E and RI

Action	**Records**
Remove animals with MW_E of less than 300 kg	13841
Remove animal with MW_E of 812 kg	13840
Remove records with RI > 130	13829
Remove records with RI < 76	13692
Remove records of breeders with less than < 50 records	12549

3.3.1. Geographic relationship between the location of the breeders, cow size and reproduction

A cluster analysis was performed on the median of MW_E and RI per breeder using PROC CLUSTER and the results visualised using PROC TREE. The geographic location of each herd in every cluster was then graphically depicted on a South African map with Maptitude 4.5 software.

3.3.2. Influence of production region and breeder on Bonsmara production traits

To investigate the influence of breeder and bioregion on BW_E, WW_E, 12 MW_E, 18 MW_E, MW_E, AFC_E, ICP_E and RI an ANOVA was performed using PROC GLM with the least square means (LSM) option. Assessment was performed at a significant level of 95% ($p \leq 0.05$) for the critical values of the F-statistic. Standard error of the means (SE) was also investigated.

3.3.3. Influence of environmental characteristics on Bonsmara production traits

A suite of stepwise regressions was performed using PROC REG with the growth variable (BW_E, WW_E, 12 MW_E, 18 MW_E), size (MW_E) and reproduction traits (AFC_E, ICP_E, RI) as dependent variables and the environmental characteristics (temperature, rainfall, soil P, soil pH, soil carbon content, CEC and grazing capacity) as explanatory variables.

The dataset was filtered prior to the analysis to remove any growth, size or reproduction trait measurements and or environmental characteristics of less than or larger than three standard deviations (SD) from the mean of each respective variable in an attempt to normalise the data. MW_E and RI were not filtered, as they were filtered in the first round of data preparation. The removal of what was considered to be extreme environmental characteristics, characteristics far removed from the norm, reduces the bias inherently occurring in the herds of individual breeders (herd effect). Although the dataset was consequently greatly reduced from 12 549 records to 5 520 records the results of the stepwise regression did not change to a great extent although the R^2 (goodness of fit) values of the models improved slightly.

3.3.4. Relationship between cow size and reproduction efficiency

The relationship between Bonsmara mature cow mass (MW_E) and reproduction (RI) was investigated by means of PROC REG. The relationship was investigated within production region (bioregion) and across production regions.

CHAPTER 4
CLASSIFICATION SYSTEM OF BEEF PRODUCTION REGIONS

4.1. INTRODUCTION

The South African National Land Type survey (1972-2002) and various vegetation classification systems (Acocks, 1988; Low & Rebello, 1996; Mucina & Rutherford, 2006) were investigated for suitability to use as a classification of beef production regions.

Land type survey

The National Land Type survey (1972-2002) was done to determine the agricultural potential of the South African soils. All relevant information such as terrain, soils and climate were taken into consideration when the maps were compiled. The first category that was defined is terrain types; i.e. areas displaying similar physical attributes. Secondly, soil types were classified into pedosystems. Climatic zones were then mapped separately and superimposed upon the pedosystems map to define land types. Land types (mapped on a scale of 1:250 000) display a marked degree of uniformity with respect to terrain form, soil pattern and climate. Each land type differs from the other in terms of one or more terrain form, soil type and climate. Land types are not distributed evenly, but are interspersed by other and different land types (Land-type-survey-staff, 1972-2010).

The land-type inventory was completed using other data collected during the survey. The complete land-type survey consisted of 69, 1:250 000 maps, with a total of 7 071 land types. A general classification system consisting of 28 broad soil patterns, 19 generalised soil patterns and nine soil groups were introduced to develop an overall soil map for the country (Land-type-survey-staff, 1972-2010). The information gathered during the land-type survey did not include the exact demarcation of soil boundaries, but focused rather on a degree of uniformity in terms of soil patterns, terrain and climate (Collett, 2008a).Owing to the large number of land types (7 071) it is impractical to use land type as an environmental classification system for the purpose of the study.

Vegetation classification systems

The vegetation of South Africa can either be considered in terms of the production characteristics of the different plant communities in the form of their grazing season and production potential or types of plant communities (Tainton, 1999). At a global scale the vegetation of the world can be described in terms of six floristic regions. The distinction between regions is based on distinctive suites of flowering plants (Anon, 2011). On a national level vegetation groupings called “biomes” are described on the basis of the dominant forms of plant life and prevailing climatic factors. Biomes broadly correspond with climatic regions. A biome has a distinct general plant appearance that makes it easy to recognise (Anon, 2011). On smaller scale vegetation type is used to group vegetation into classes. Vegetation type is usually harder to recognise. It is defined in terms of dominant, common, as well as rare plant species, as well as its association with landscape features such as soil or geology, topography and climate (Anon, 2011).

4.2. RESULTS

The objective classification of beef production regions is challenging. The livestock production region map developed by Bonsma & Joubert (1957) identified production regions suitable for different types of livestock. Their map is shown in Figure 2.1. According to Bonsma & Joubert (1957) a sound knowledge of the geographical and physical features of the various production regions is necessary and each production region’s potential to provide favourable conditions for the expression of the animal’s inherent productive ability must be taken into account in order to describe a livestock production region. Tainton *et al*. (1993) suggested on a similar note that it is possible to classify the South African beef production areas on the basis of the structure and composition of the vegetation or its seasonal use classes.

The literature study indicated that the environmental characteristics that have the largest influence on animal production can be divided into climatic factors, soil factors, and forage production characteristics as well as nutritional constraints. Rainfall, temperature, CEC, soil pH, soil organic matter, season of forage use, grazing capacity, vegetation composition and P content of the soil were all shown to have either a direct or indirect effect on animal production. The environmental classification system chosen to act as a beef production region classification system should accordingly be based on as many of these factors as possible. It stands to reason that the classification system should also make geographically sense and that the classification system should be compiled from a large database of recent environmental information. The distribution of Bonsmara breeders should also fit the distribution on the regions identified by the classification system. The following is a synopsis of the current South African environmental classification systems that were evaluated for suitability as a classification system of beef production regions.

4.2.1. Acocks

Acocks initiated a national vegetation survey in 1945 based on the 1:1500000 postal communications map (Acocks, 1953). Acocks travelled throughout South Africa during a 40-year period and sampled some 3 300 vegetation sites on the basis of which he described vegetation patterns at vegetation level, based on the agricultural potential of the vegetation (Low & Rebelo, 2000).

Acocks veld-types

Acocks (1988) described a veld-type as “a unit of vegetation whose range of variation is small enough to permit the whole of it to have the same farming potentialities”. The term “veld-type” can be widely interpreted but, as a vegetation unit, the variation is limited to the relative importance of members of a group of species occurring through its area (Acocks, 1988). Acocks described 70 major veld-types with 75 variations within the different veld-types. The Acocks veld-type map is shown in Figure 4.1. The 11 major veld groupings published in Botanical Survey Memoir No. 57 (Acocks, 1988) was digitised by the ARC-Institute for Soil Climate and Water (ARC-ISCW) and is depicted in Figure 4.2 (AGIS., 2010).

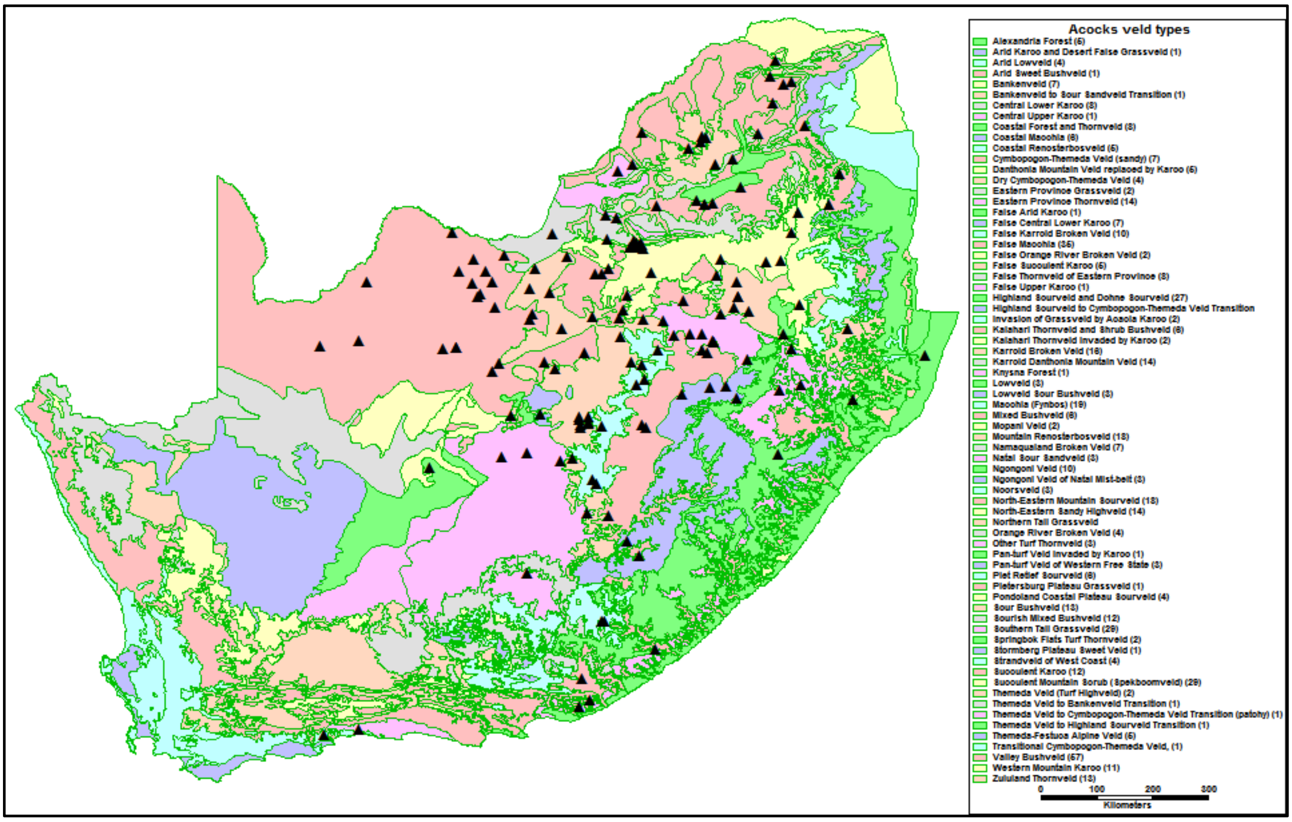

Figure 4.1 Location of Bonsmara breeders based on the veld-types of Acocks (1988) (indicated with triangles)

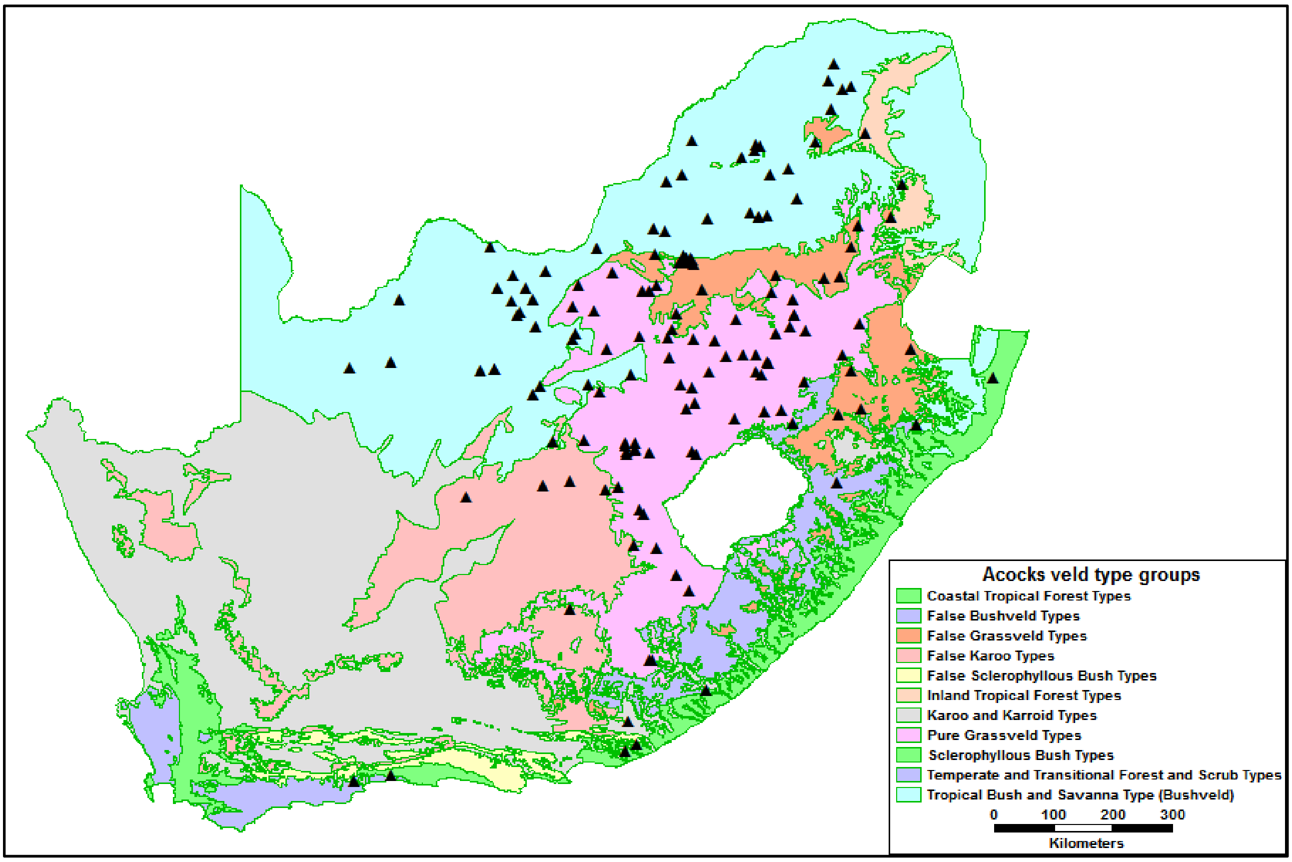

Figure 4.2 Location of Bonsmara breeders based on the veld-type groupings of Acocks (1988) (indicated with triangles)

4.2.2. Low & Rebelo

In 1992 a vegetation classification system project was launched by Low & Rebelo (1996) to replace the classic Acocks classification system. Where the Acocks system focused on the agricultural potential of the vegetation types, the new system was intended for a wider range of use. A more modern approach of vegetation mapping was introduced and more recent data was incorporated into the map (Low & Rebelo, 2000).

Low & Rebelo biome classification system

Low & Rebelo (1996) define a "biome" as a broad ecological unit that represents the major life form zones of large natural areas. In the South African context biomes are mostly defined by vegetation and structure. Seven different biomes were identified by using this system (Low & Rebelo, 1996).

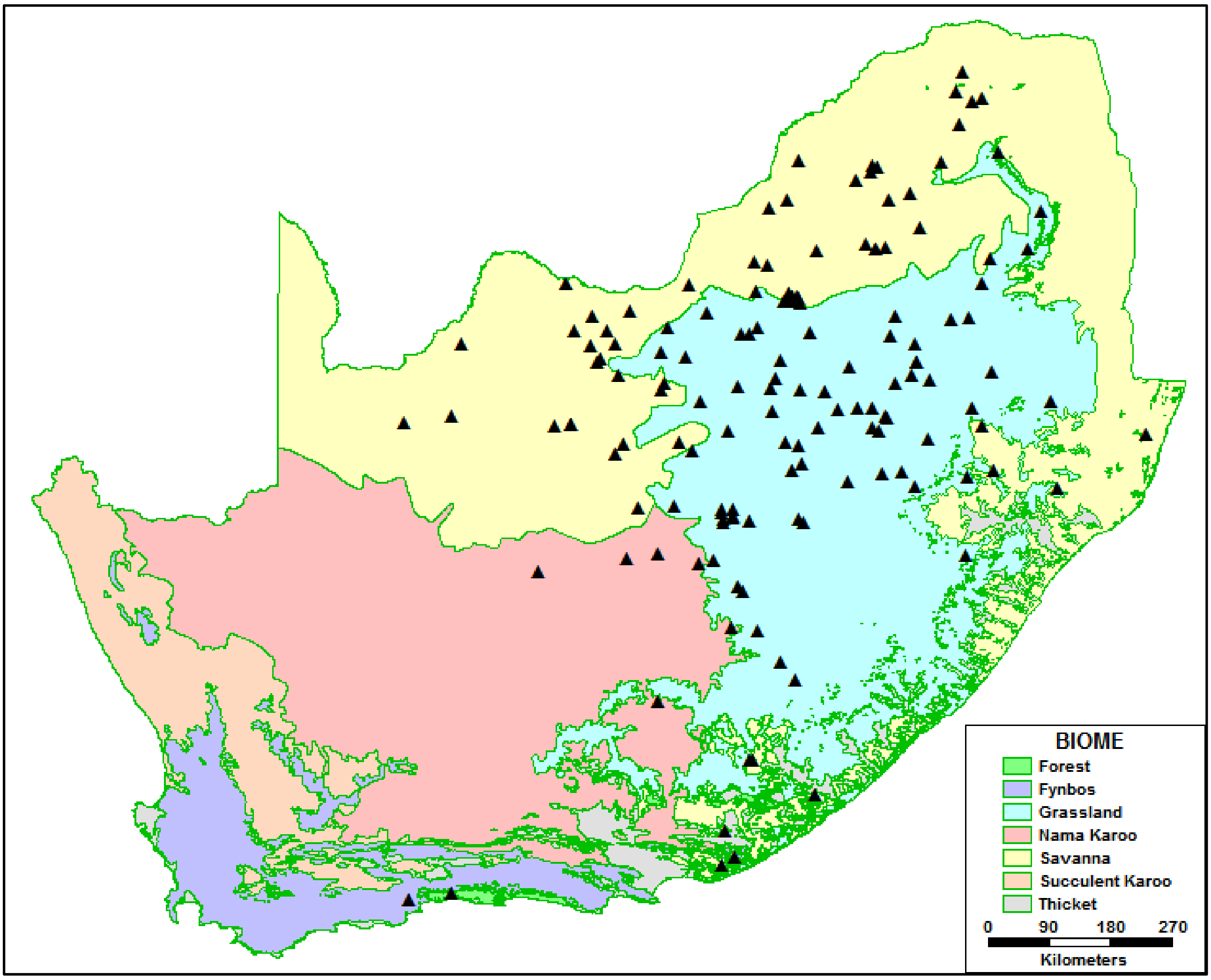

Figure 4.3 Location of Bonsmara breeders based on the biomes of Low & Rebelo (1996) (indicated with triangles)

Low & Rebelo vegetation types

Vegetation types are described by Low & Rebelo (1996) as vegetation communities defined by their structure and composition and share similar climatic, geological and soil requirements. Low & Rebelo state that a vegetation type should also be subject to similar ecological processes, management and conservation requirements as well as potential uses. The Low & Rebelo vegetation classification system identified 68 different vegetation types (Low & Rebelo, 1996).

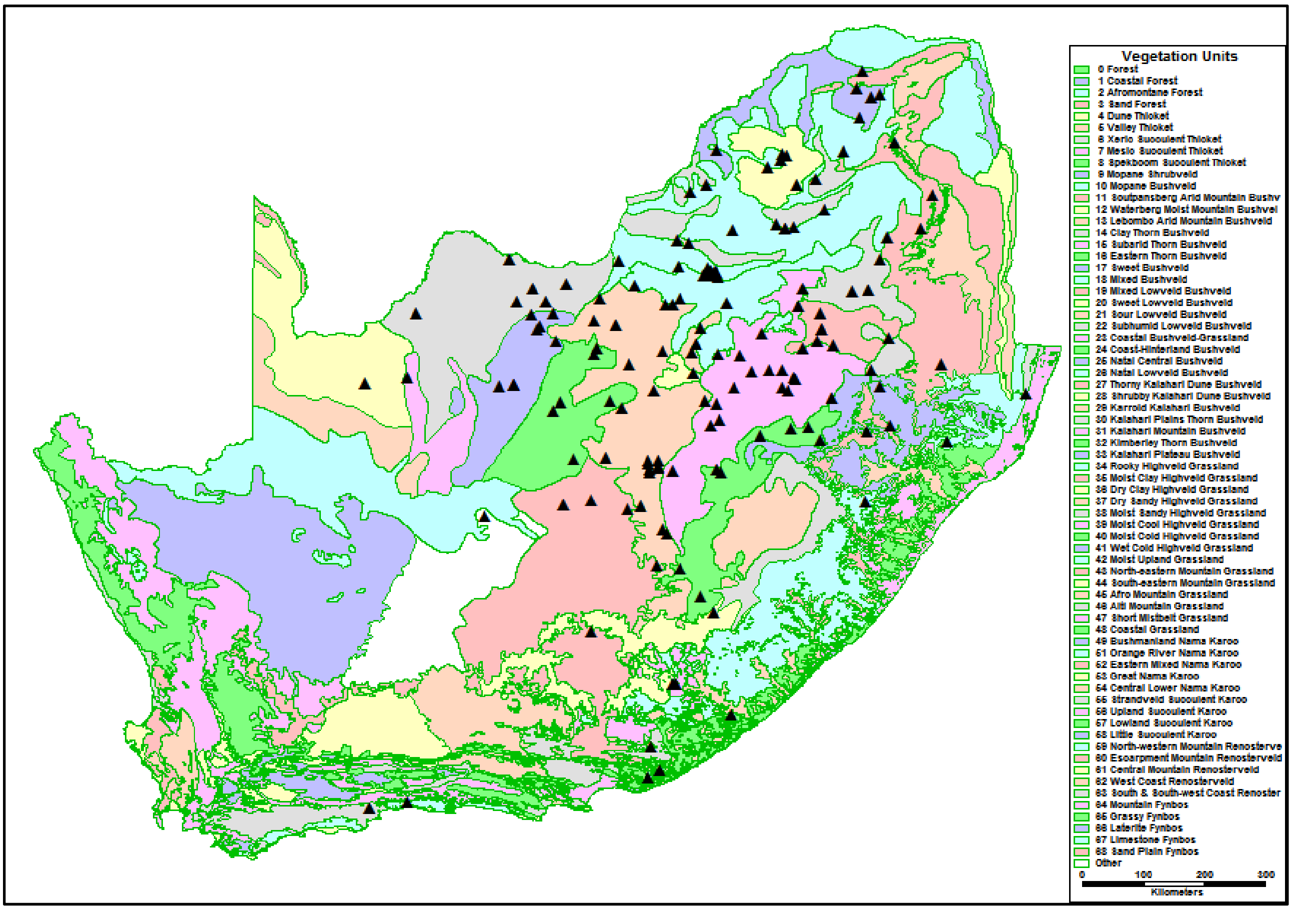

Figure 4.4 Location of Bonsmara breeders based on the vegetation units of Low & Rebelo (1996) (indicated with triangles)

4.2.3. VEGMAP

VEGMAP is the latest South African vegetation classification map introduced by Mucina & Rutherford in 2006. It makes use of three main classification units', viz. vegetation composition-biomes, bioregions and vegetation types. The aim of VEGMAP was to produce a map "that features vegetation units represented in simplified form to create a graphical special model of vegetation of the region". VEGMAP was compiled with the help of GIS-tools and incorporated aerial photography, satellite imagery, spatial predictive modelling in combination with traditional field-based ground-truthing (Mucina & Rutherford, 2006).

VEGMAP biomes

Mucina & Rutherford (2006) use a similar definition for a "biome" to that of Low & Rebelo (1996). Mucina & Rutherford (2006) describe biomes as simplified units that have similar vegetation structures, which are exposed to the same macroclimatic patterns. Biomes are not characterised by individual species but mainly by emergent properties of vegetation structure and associated climate. According to the authors, the quantitative link between climate and life forms serves as a basis for constructing biomes. VEGMAP describes nine biomes, two more than Low & Rebelo (1996).

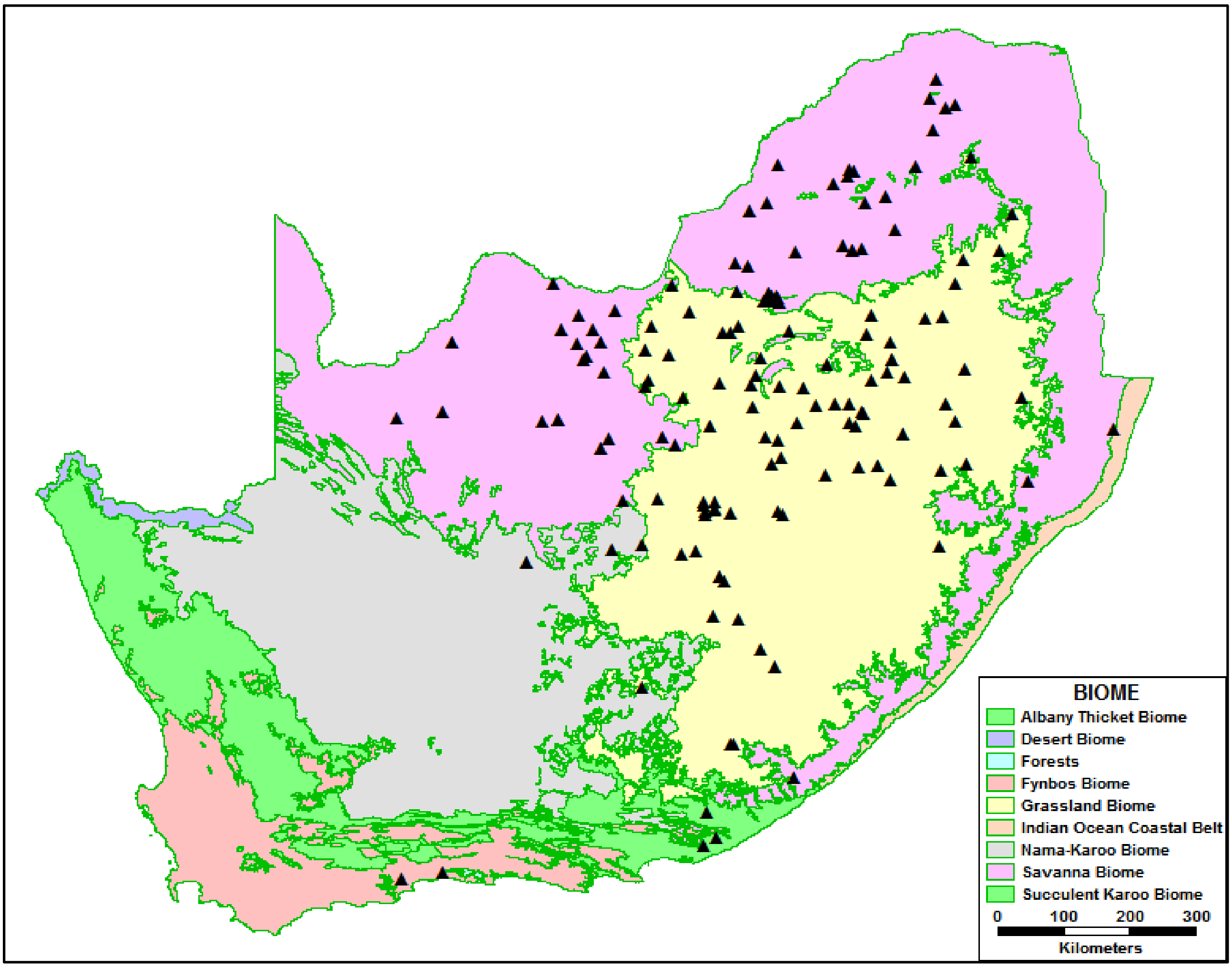

Figure 4.5 Location of Bonsmara breeders based on the biomes of VEGMAP (indicated with triangles)

VEGMAP bioregions

The bioregion classification was first used by Mucina & Rutherford (2006) and is a taxon between a biome and a vegetation unit. A bioregion is described by Mucina & Rutherford (2006) as a composite special terrestrial unit that is defined on the basis of similar biotic and physical features and processes on a regional scale. The focus of bioregions is on the floristic composition of their component vegetation types. Bioregions are furthermore divided into climatic entities with relative similar climates within the bioregions; there are usually distinct differences in climate between bioregions. VEGMAP describes 35 bioregions (Mucina & Rutherford, 2006).

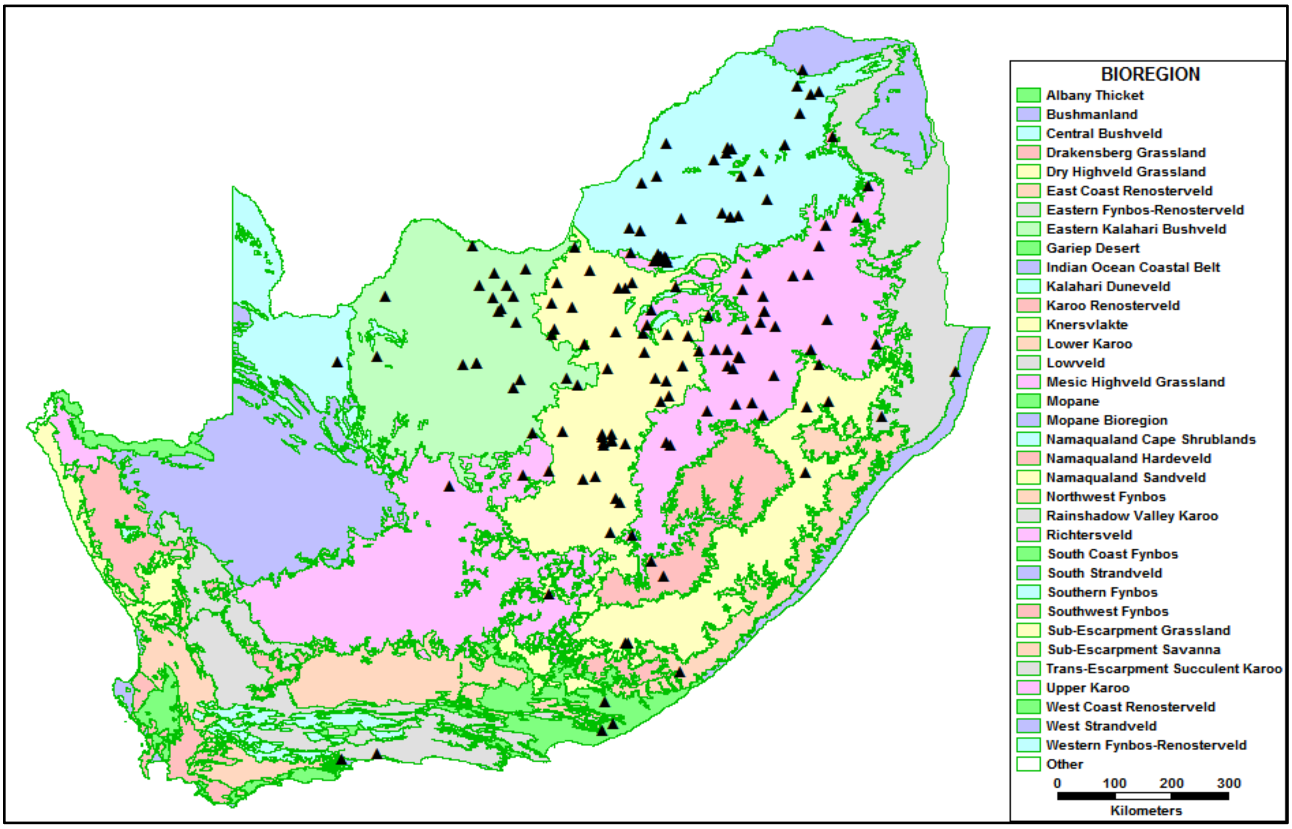

Figure 4.6 Location of Bonsmara breeders based on the bioregions of VEGMAP (indicated with triangles)

VEGMAP's vegetation types

Vegetation units are described by Mucina & Rutherford (2006) as vegetation complexes that share some general ecological properties such as their position on major ecological gradients as well as nutrient levels that appear similar in vegetation structure. VEGMAP describes 435 different vegetation types (Mucina & Rutherford, 2006).

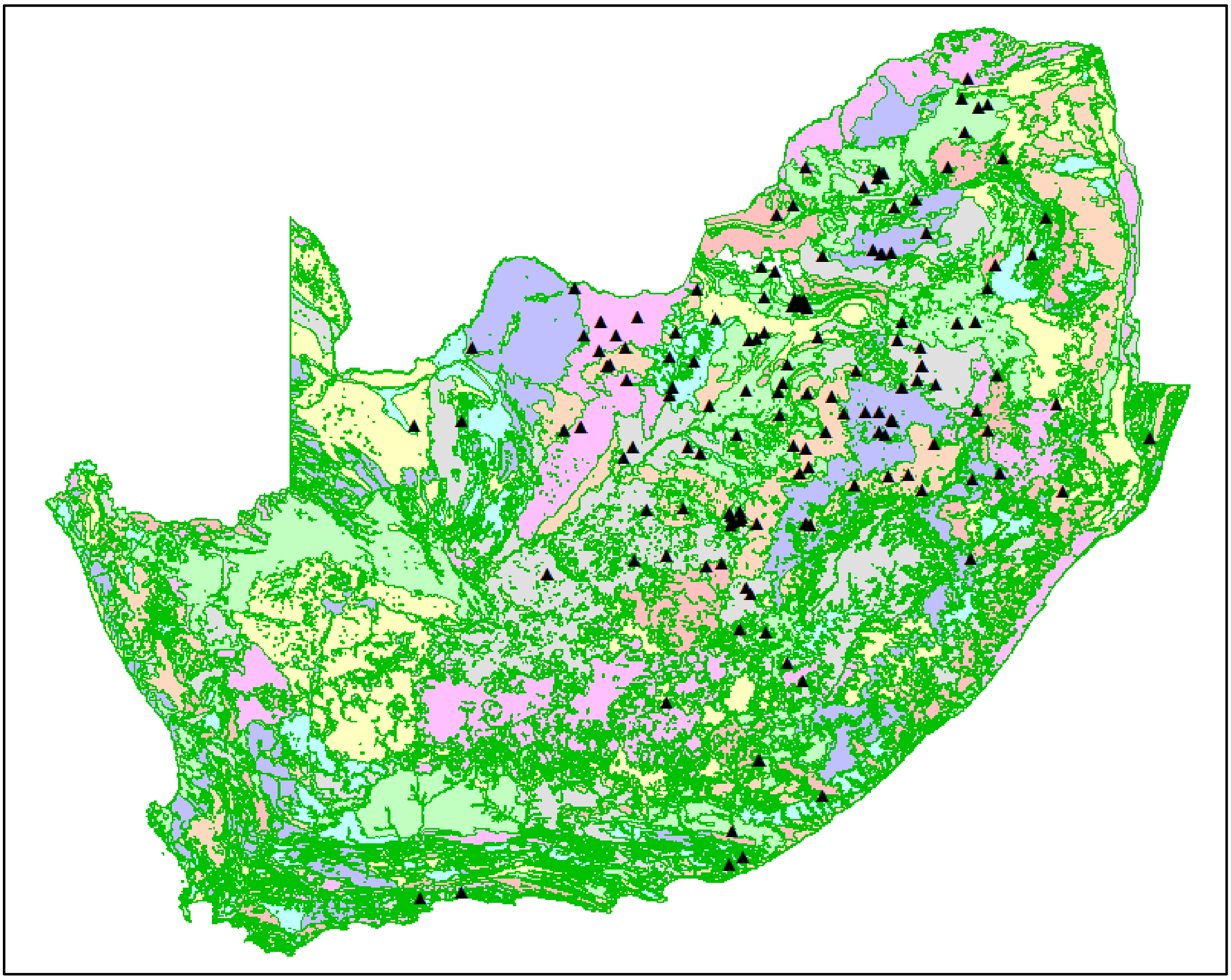

Figure 4.7 Location of Bonsmara breeders based on the vegetation types of VEGMAP (indicated with triangles)

4.3. DISCUSSION

4.3.1. Identification of beef production regions

The aim of this investigation was to evaluate the suitability of existing environmental classification systems for use as a classification system of beef production regions. The two older vegetation classification systems by Acocks (1988) and Low & Rebelo (1996) were deemed less accurate due to more limited input data than the newer VEGMAP classification system. The aforementioned were thus discarded because VEGMAP is based on more detailed data, which increases the chance for statistical correlations.

The VEGMAP classification system by Mucina & Rutherford (2006) is currently South Africa's most accurate and up to date environmental classification system. The map compilers had access to a large database of vegetation site- and remote sensed spatial information. When the localities of Bonsmara breeders were superimposed on the three VEGMAP classification systems (biome, bioregion and vegetation type) it was clear that the biome and vegetation type classification are unsuitable to use for the purpose of this study. Figure 4.5 indicates that the majority of the Bonsmara breeders are located in only two of the nine biomes. The scale of the biome classification system is therefore too large to be suitable for this study. The large number of vegetation types and the geographically scattered nature of the vegetation type classification units, shown in Figure 4.7, make the vegetation type classification units unsuitable as a production region classification system for Bonsmara cattle. The bioregion classification system, shown in Figure 4.6, is visually a more suitable classification system.

It would appear as if the VEGMAP bioregion classification fits most of the criteria identified as necessary for a production region classification system for Bonsmara cattle. The bioregions are classified on the basis of environments with similar biotic and physical features (Mucina & Rutherford, 2006). Although the authors were not specific which biotic and physical features were used to classify the bioregions, it can be assumed that at least some of the environmental characteristics that influence animal production were included.

The four bioregions into which the majority of Bonsmara breeders fall display similarities to some of the production regions classified by Bonsma & Joubert (1957), as shown in Figure 2.1. The Central Bushveld bioregion is geographically similar to the Northern Transvaal ranching area; the Eastern Kalahari Bushveld corresponds roughly with the Bechuanaland ranching area; the Dry Highveld Grassland bioregion displays some correlation with the semi-intensive cropping and livestock production area and the Mesic Highveld Grassland bioregion is very similar to the intensive cropping and ranching area. The similarities are remarkable and accolades to the pioneering work of Bonsma & Joubert in 1957. Their hand-drawn maps, based on experience and the information on available environmental characteristics at that time, are very similar to the latest vegetation classification maps drawn by GIS software.

The similarity between the livestock production areas map of Bonsma & Joubert (1957), which was designed to predict animal performance and the bioregion classification system according to VEGMAP, is the main support for the use of bioregion as the production region classification system for the purpose of this study. The bioregion classification system of Mucina & Rutherford (2006) is therefore the most suitable environmental classification system available that could be used to predict extensive beef cattle performance in South Africa, with specific reference to Bonsmara cattle.

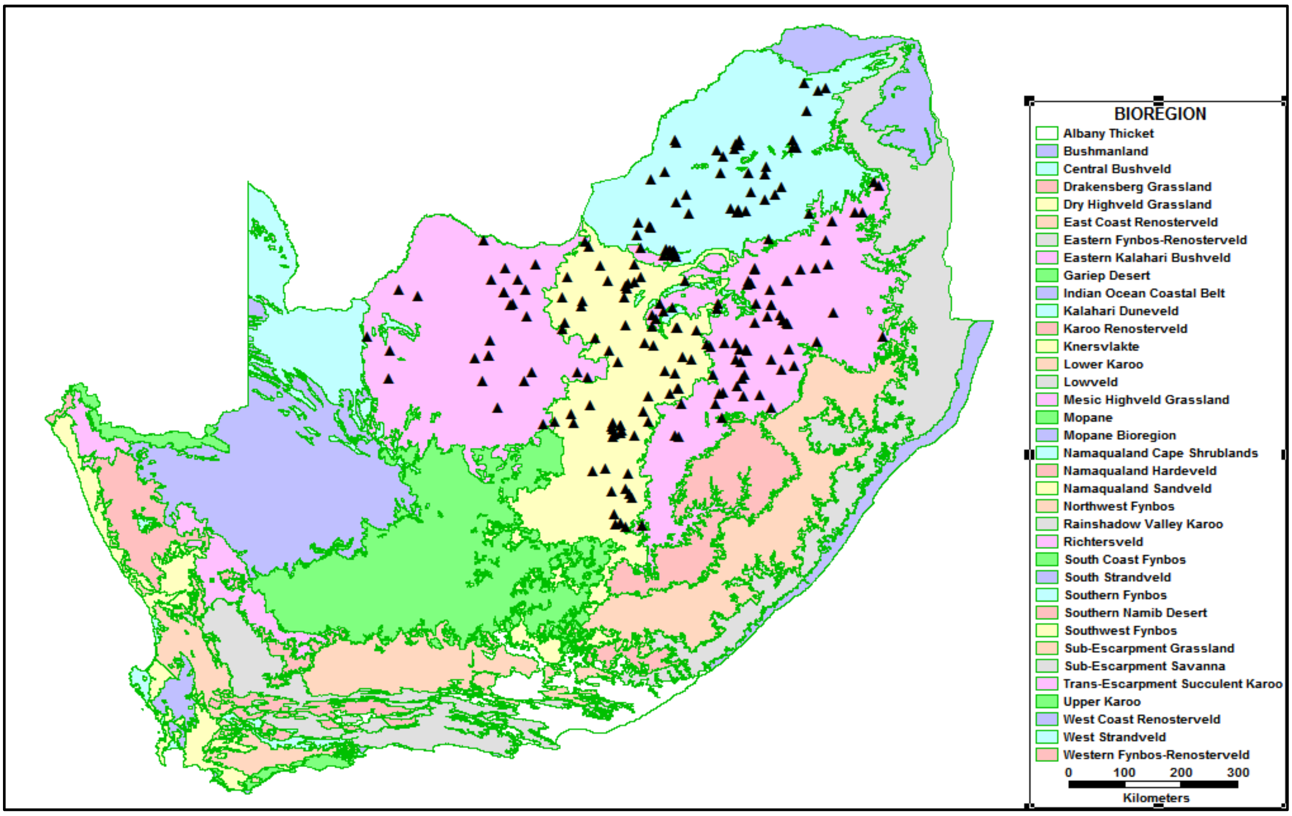

Figure 4.8 Bonsmara breeder locations in the Central Bushveld-, Eastern Kalahari Bushveld-, Dry Highveld Grassland- and Mesic Highveld Grassland bioregions of South Africa

CHAPTER 5
EFFECT OF PRODUCTION REGION ON THE PRODUCTION EFFICIENCY OF BONSMARA COWS

5.1. INTRODUCTION

The effect of the production environment on cow size and efficiency has been investigated by numerous authors (Cundiff *et al*., 1966; Dooley *et al*., 1982; Leighton *et al*., 1982; Burfening *et al*., 1987; Ronchietto, 1993; Botsime, 2005; Nqeno, 2008). It is generally agreed that the efficiency of a beef cow is significantly affected by her production environment. Cows that are of optimal size for their environment are generally expected to be the most efficient producers (Kattnig *et al*., 1993). The influence of the production environment on Bonsmara cow efficiency was determined by investigating the influence production region (defined as VEGMAP's bioregions) has on Bonsmara production traits. Summary statistics of the production traits investigated are presented in Table 5.1. Bonsmara breeders believe that there is a tendency for Bonsmara cows in the eastern part of the country to be smaller and less reproductive than those in the western parts of the country. It should be noted that for the purpose of this study "breeder" or farmer means in effect "location".

Table 5.1 Summary statistics for the production traits investigated

Traits	N	Mean	S.D	S.E.M	Median	Mode
BW_E	12185	34.3	3.4	9.9	34.3	38.0
WW_E	12549	214.7	31.3	14.6	214.7	252.2
12 MW_E	11524	254.6	39.4	0.4	253.8	166.7
18 MW_E	9689	329.1	45.8	0.5	328.3	255.9
MW_E	12549	499.5	54.4	0.5	498.6	568.5
AFC_E	12549	963.9	115.9	1.0	954.7	715.0
ICP_E	9016	422.8	62.3	0.7	407.7	.
RI	12549	104.6	8.9	0.1	105.8	96.7

BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period
RI	Reproduction index

5.2. RESULTS & DISCUSSION

5.2.1. Effect of geographic location on the size of Bonsmara cows

Cluster analysis was performed to investigate the effect that geographic location has on Bonsmara cow size. Breeders were clustered by means of PROC Cluster according to their median herd MW_E. The dendogram shown in Figure 5.1 indicates that there are four clusters of breeders with a distance of 0.8 between the cluster centroids.

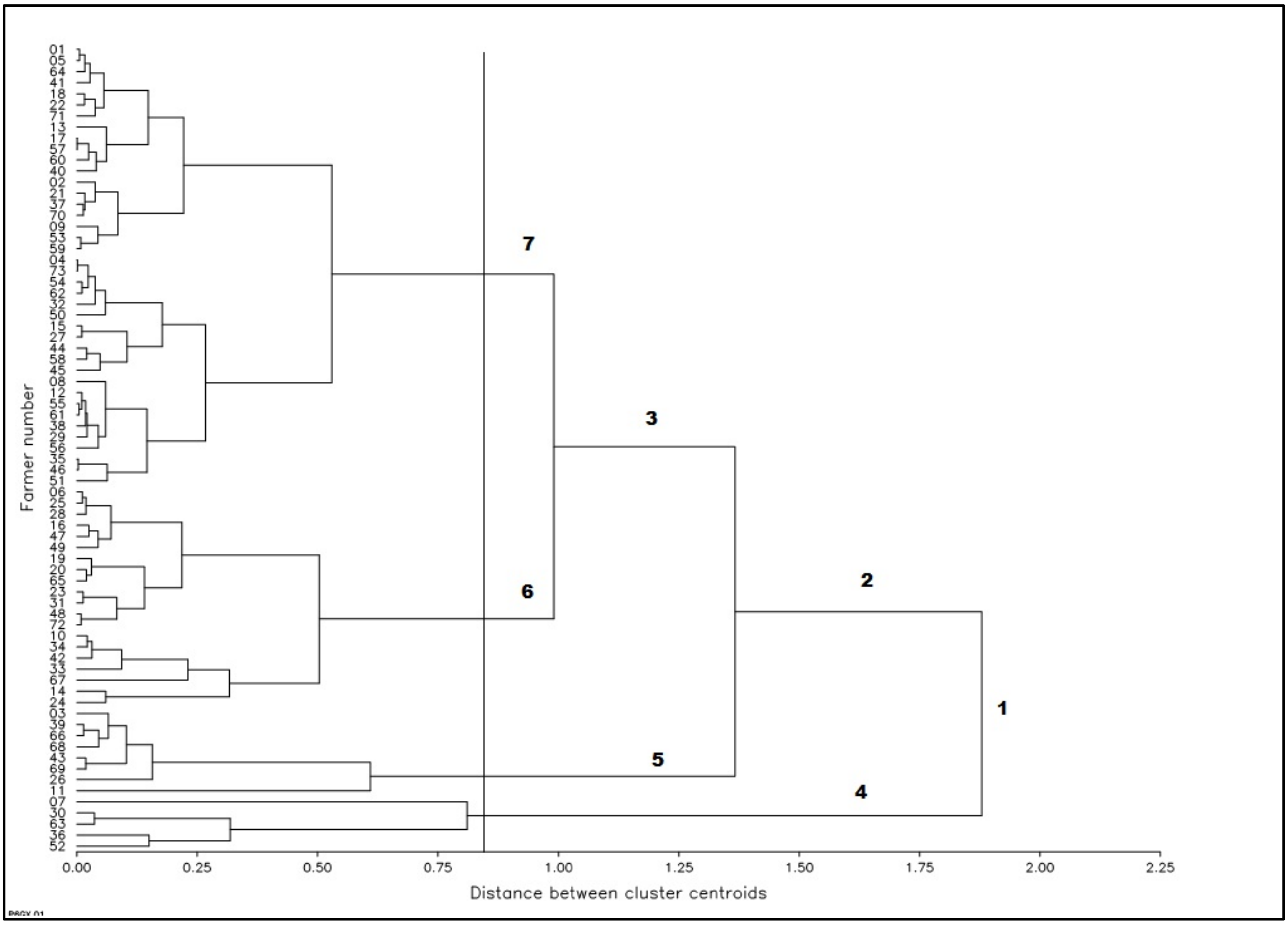

Figure 5.1 Clustering of breeders for the median of MW_E

Summary statistics for the number of animals and herds within a cluster as well as the median MW_E for the four clusters are presented in Table 5.2. In order to objectively assess the geographic distribution of herds located within a cluster (cluster component herds) a summary of the number of cluster component herds per bioregion is given in Table 5.3. The geographic locations of the cluster component herds are shown in Figure 5.2.

Table 5.2 Summary of cluster contents for MW_E

Cluster #	# Animals	# Herds	Median	Distance
Cluster 4	429	5	427.4 kg	0.81
Cluster 7	3600	20	471 kg	0.50
Cluster 6	7751	40	509.6 kg	0.53
Cluster 5	769	8	550.7 kg	0.61

From Figure 5.1 and Table 5.2 it is evident that there are not many herds with a median MW_E that deviate far from the database MW_E average of 499.5 kg. When the geographic distribution of the cluster component herds, presented in Figure 5.2, and the summary of the cluster component herd's occurrence per bioregion, which are presented in Table 5.3, are studied, it would appear as if there is a non-convincing tendency for herds with smaller-sized cows to occur in the eastern and northern parts of the country.

Table 5.3 Geographic location of cluster component herds per bioregion

	Central Bushveld	Dry Highveld Grassland	Eastern Kalahari Bushveld	Mesic Highveld Grassland	Total
Cluster 4	1	-	-	4	5
Cluster 7	8	1	2	9	20
Cluster 6	7	14	11	8	40
Cluster 5	2	2	2	2	8
AVG MW_E	494.3 kg	512.3 kg	506.3 kg	488.1 kg	499.5

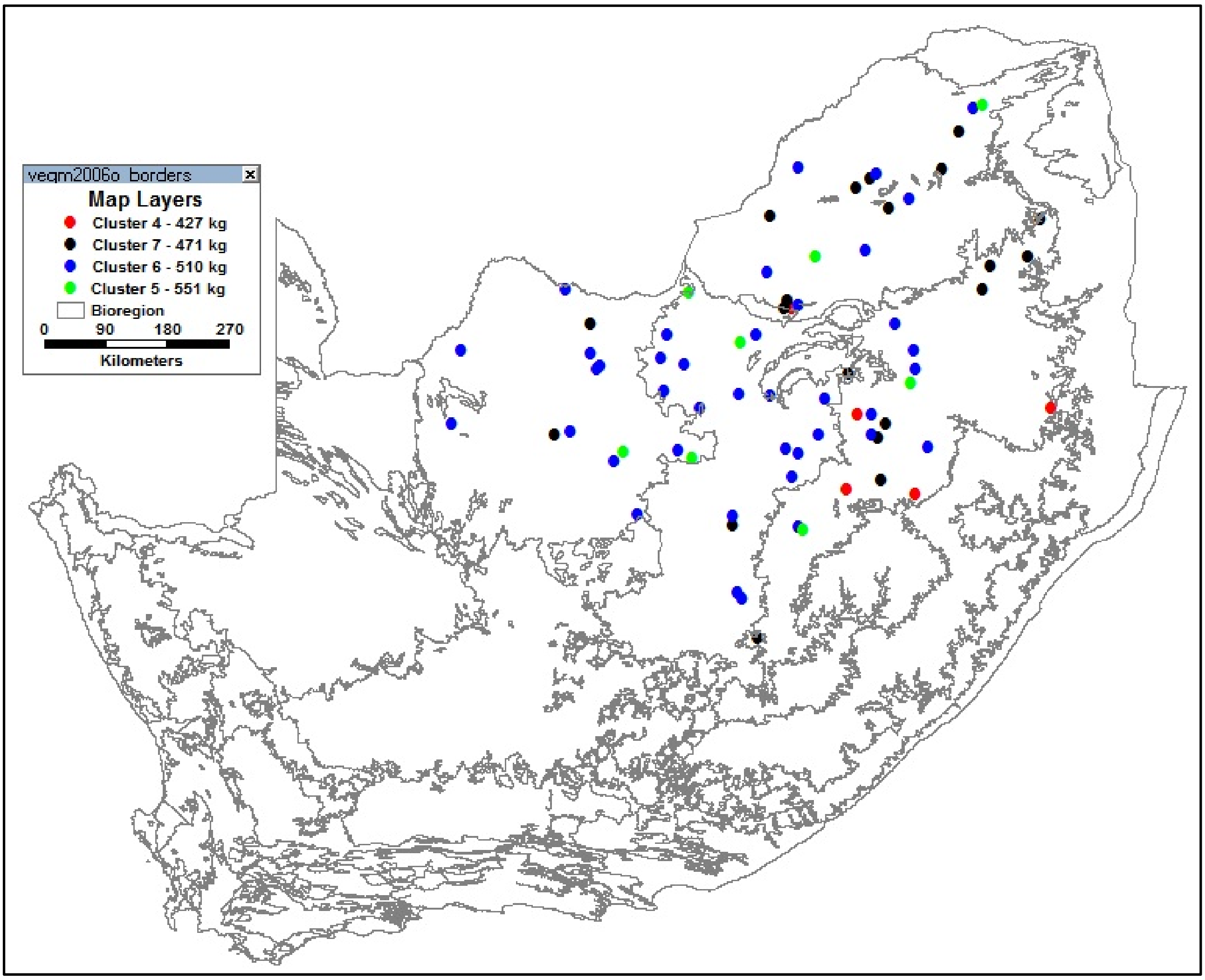

Figure 5.2 Geographic locations of the cluster component herds

Table 5.3 indicate that the Mesic Highveld Grassland, located in the eastern part of the country, is the production region with the numerical lowest average median MW_E mass (488.1 kg). Four of the five herds contained in the cluster with the lowest MW_E median (Cluster 4) and nine out of 20 herds with the numerically second lowest MW_E median's MW_E (Cluster 7) are located in the Mesic Highveld Grassland bioregion. The Central Bushveld bioregion, located in the northern part of the country, is the production region with the second lowest average numerical median MW_E (494.3 kg). One of the five herds grouped in cluster 4 and eight of the 20 herds grouped in cluster 7 are located in the Central Bushveld.

The geographic distribution of some of the herds that are grouped in clusters 4 and 7 (herds with lower MW_E medians) would seemingly support the belief that Bonsmara cows in the eastern parts of the country are smaller than those cows that are found in the western parts of the country. However, the herds grouped by higher MW_E medians, clusters 5 and 6, are geographically evenly dispersed between all the bioregions. An objective conclusion regarding the influence that geographic location has on Bonsmara cow size can therefore not be drawn from the cluster analysis.

5.2.2. Effect of production region on the growth and size of Bonsmara cows

The effects of production region and breeder on the growth, size and reproduction traits of Bonsmara cows were investigated by ANOVA. Examples of ANOVA based on PROC GLM are given in Tables 5.4 and 5.5.

Table 5.4 Example of PROC GLM output for the effect of bioregion on MW_E

```
                                   The GLM Procedure
                                Class Level Information

                      Class          Levels     Values
                      Bioregion        4     Cent-Bush Dry-Highl East-Kala Mesic-HV

               Data for Analysis of MW_E

                              Number of Observations Read       12549
                              Number of Observations Used       12549
Dependent Variable: MW_E
                                                                Sum of
       Source                       DF         Squares      Mean Square     F Value     Pr > F
       Model                         3      1154698.99        384899.66      134.41     <.0001
       Error                     12545     35923230.86          2863.55
       Corrected Total           12548     37077929.85

               R-Square      Coeff Var       Root MSE       V22 Mean
               0.031142      10.71392        53.51215       499.4637

       Source                       DF     Type III SS      Mean Square     F Value     Pr > F
       Bioregions                    3     1154698.991       384899.664      134.41     <.0001

                                                  Standard                         LSMEAN
               Bioregion      MW_E LSMEAN            Error      Pr > |t|          Number
               Cent-Bush       494.311915         1.100132        <.0001               1
               Dry-Highl       512.294069         1.076287        <.0001               2
               East-Kala       506.268711         0.874199        <.0001               3
               Mesic-HV        488.104841         0.849935        <.0001               4

                              Least Squares Means for effect bioregion
                              Pr > |t| for H0: LSMean (i) =LSMean (j)

                              Dependent Variable: MW_E
               i/j         1              2              3              4

               1                       <.0001         <.0001         <.0001
               2        <.0001                        <.0001         <.0001
               3        <.0001         <.0001                        <.0001
               4        <.0001         <.0001         <.0001
```

Table 5.5 Example of PROC GLM for the effect of breeder on MW_E

```
                              The GLM Procedure
                           Class Level Information

Class Levels Values

V1 73   28686 29158 31417 31853 44121 68049 79208 108682 112089 115558 119459 293570 296170 298377
        298988 304311 310254 319398 319818 320409 320424 322973 330990 332178 332218 336568 337014
        339136 340481 340697 340709 342662 347319 349556 349571 357028 357084 365032 365711 378288
        389342 397182 406026 406421 408887 443131 453940 454684 460261 460482 464271 474439 475007
        476078 479316 482808 496895 500144 504004 505767 507228 512224 516518 520104 522258 523817
        527107 545391 548939 556018 556399 560337 571511

                           Data for Analysis of MW_E

                    Number of Observations Read       12549
                    Number of Observations Used       12549

Dependent Variable: MW_E
                                            Sum of
        Source                   DF        Squares     Mean Square    F Value    Pr > F
        Model                    72     9647038.61       133986.65      60.94    <.0001
        Error                 12476    27430891.24         2198.69
        Corrected Total       12548    37077929.85

                      R-Square     Coeff Var      Root MSE      V22 Mean
                      0.260183      9.388115      46.89022      499.4637

        Source                   DF    Type III SS     Mean Square    F Value    Pr > F
        Breeder                  72    9647038.611      133986.647      60.94    <.0001
```

A summary of the proportions of variation explained by bioregion and breeder (R^2) are presented in Table 5.6. The LSM for the different growth and size traits are presented in Table 5.7. Summary statistics for the four bioregions are presented in Table 5.8.

Table 5.6 Summary of R^2 values for the production traits of Bonsmara cows

	R^2	
Trait	**Breeder**	**Bioregion**
BW_E	0.12	0.01
WW_E	0.21	0.08
12 MW_E	0.30	0.07
18 MW_E	0.24	0.03
MW_E	0.26	0.03
AFC_E	0.23	0.03
ICP_E	0.16	0.02
RI	0.22	0.05

BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period
RI	Reproduction index

Table 5.7 LSM (LSM ± S.E) for growth and size traits per bioregion

Bioregion	BM_E LSM	S.E	WM_E LSM	S.E	12 MW_E LSM	S.E	18 MW_E LSM	S.E	MW_E LSM	S.E
Central Bushveld	34.0 [a]	0.07	206.9 [a]	0.62	249.8	0.81	319.8 [a]	1	494.3	1.1
Dry Highveld	34.5 [b]	0.07	216.5	0.6	261.2	0.79	332.4	1.06	512.3	1.08
Eastern Kalahari	34.7 [b]	0.06	227.2	0.49	266.1	0.64	340.3	0.85	506.3	0.87
Mesic Highveld	33.9 [a]	0.05	206.5 [a]	0.48	241.4	0.65	322.9 [a]	0.82	488.1	0.85

Least Square Means with same superscript do not differ statistically significantly ($p > 0.05$)

S.E	Standard Error
LSM	Least square means
Central Bushveld	Central Bushveld bioregion
Dry Highveld	Dry Highveld Grassland bioregion
Eastern Kalahari	Eastern Kalahari Bushveld bioregion
Mesic Highveld	Mesic Highveld Grassland bioregion
BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight

Table 5.8 Summary statistics for the Bonsmara cow production traits in the four bioregions

Bioregion	n	Variable	n	Mean	Std Dev	Std E	Variance	Min	Max
Central Bushveld	2366	BW_E	2213	33.99	3.23	0.07	10.46	21.52	45.46
		WW_E	2366	206.91	29.82	0.61	889.04	107.49	353.34
		12 MW_E	2197	249.77	39.09	0.83	1528.06	122.88	431.08
		18 MW_E	2022	319.80	45.83	1.02	2100.00	189.07	573.92
		MW_E	2366	494.31	53.08	1.09	2817.33	343.07	717.55
		AFC_E	2366	980.27	105.56	2.17	11143.82	516.60	1170.19
		ICP_E	1668	420.47	60.17	1.47	3620.00	327.71	680.99
		RI	2366	103.53	9.29	0.19	86.32	76.47	127.44
Dry Highveld Grassland	2472	BW_E	2438	34.51	3.63	0.07	13.17	20.06	47.97
		WW_E	2472	216.54	29.59	0.60	875.81	111.28	298.58
		12 MW_E	2352	261.21	38.16	0.79	1455.87	152.33	406.48
		18 MW_E	1804	332.35	46.63	1.10	2174.47	186.96	480.35
		MW_E	2472	512.29	49.26	0.99	2426.06	356.95	709.80
		AFC_E	2472	957.99	106.83	2.15	11413.43	682.44	1162.52
		ICP_E	1833	412.65	56.10	1.31	3147.39	328.22	685.10
		RI	2472	106.20	7.77	0.16	60.32	77.69	129.62
Mesic Highveld Grassland	3964	BW_E	3821	33.92	3.52	0.06	12.40	18.45	48.55
		WW_E	3964	206.50	29.48	0.47	869.35	99.54	301.30
		12 MW_E	3466	241.44	40.22	0.68	1617.69	136.59	406.89
		18 MW_E	3050	322.89	45.65	0.83	2084.06	183.12	470.16
		MW_E	3964	488.10	58.04	0.92	3369.18	312.19	695.76
		AFC_E	3964	985.17	125.52	1.99	15755.52	443.99	1173.30
		ICP_E	2621	436.38	71.23	1.39	5073.97	320.48	724.20
		RI	3964	102.05	9.47	0.15	89.76	76.01	129.45
Eastern Kalahari Bushveld	3747	BW_E	3713	34.68	3.17	0.05	10.07	20.21	47.76
		WW_E	3747	227.23	31.04	0.51	963.37	120.60	330.51
		12 MW_E	3509	266.07	35.13	0.59	1234.47	155.44	412.71
		18 MW_E	2813	340.32	42.60	0.80	1815.05	192.61	535.87
		MW_E	3747	506.27	51.44	0.84	2646.39	344.23	738.02
		AFC_E	3747	935.08	110.61	1.81	12233.51	513.51	1162.11
		ICP_E	2894	418.14	56.16	1.04	3153.64	328.93	691.06
		RI	3747	106.79	7.97	0.13	63.46	76.09	128.84

BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period
RI	Reproduction index

Effect of bioregion and breeder on birth weight

One-way ANOVA results, presented in Table 5.7, reveals that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component of birth weight (BW_E) for some of the bioregions. There are, however, no statistically significant differences between the Dry Highland Grassland and the Eastern Kalahari Bushveld and between the Central Bushveld and the Mesic Highveld Grassland. The proportion of variation in BW_E explained by bioregion is, however, very low (1%).

These results are similar to those of previous studies. Burfening *et al*. (1987) estimated age-of-dam effects and evaluated two-way interactions between age of dam, region, season of birth and pre-weaning management for birth weight and 205-d weight of Simmental calves in the USA. It was found that region had a statistically significant ($p < 0.05$) effect on birth weight; region, however explained only 0.25% of the variation. Botsime (2005) investigated the effect of agro-ecological region (veld-types), sex, season of birth and their interactions on anthropometrical measurements of Nguni cattle in four different locations of South Africa. It was found that veld-type had no significant effect on birth weight ($p < 0.05$).

Results, presented in Table 5.6, reveal that the effect of individual breeders on BW_E is also statistically highly significant ($p < 0.0001$). Breeder explains 12% of the variation in BW_E. The breeders, therefore, have a much larger influence on BW_E than bioregion (1%).

Effect of bioregion and breeder on weaning weight

Results, presented in Table 5.7, reveal that there are statistically significant ($p < 0.05$) differences between LSMs of the environmental component of weaning weight (WW_E) of all the bioregions. The proportion of variation in WW_E explained by bioregion is however low (8%).

These results are similar to those found in previous studies. Cundiff *et al*. (1966) examined the effects of seven environmental factors on the weaning weight of Angus and Hereford calves and the importance of two-way interactions among these factors in six areas of the Oklahoma state of the USA. Area had a significant ($p < 0.1$) effect on weaning weight, although only 5% of the variation in weaning weight was explained by area. Dooley *et al*. (1982) characterised the production ability of six cattle breeds in the South Dakota state of the USA. Region had a significant ($p < 0.05$) effect on the weaning weight of calves. Leighton *et al*. (1982) examined the relative importance of sex of calf, region, age of dam, and the two-factor interactions among these effects on the weaning weight of Hereford calves in the USA. Region had a statistically significant ($p < 0.01$) effect on weaning weight, but the actual effect of region on weaning weight was not judged to be biologically significant. Burfening *et al*. (1987), in the study previously referred to, found that region had a statistically significant effect ($p < 0.1$) on weaning weight although region only explained 0.28% of the variation. Ronchietto (1993) investigated the effect of agro-ecological region, season of birth, sex and their first order interactions on pre-wean and wean growth of commercial beef herds in the then Natal province of South Africa. Region had a statistically significant ($p <0.01$) effect on weaning weight, although only 3.4% of the variation was explained.

The effect of the individual breeder, presented in Table 5.6, on WW_E is also statistically highly significant ($p < 0.0001$). Breeder explains 21% of the variation in WW_E. Breeder therefore has a much larger influence on WW_E than bioregion (8%).

Effect of bioregion and breeder on 12-month weight

Results, presented in Table 5.7, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component of 12-month weight (12 MW_E) of all the bioregions. The proportion of variation in BW_E explained by bioregion is low (7%).

Results, presented in Table 5.6, revealed that the effect that the individual breeders had on 12 MW_E is also statistically highly significant ($p < 0.0001$). Breeder explains 30% of the variation in 12 MW_E. Breeder, therefore, has a much larger influence on 12 MW_E than bioregion (7%). The majority of the variation in 12 MW_E is, therefore, due to the influence of breeder, rather than bioregion.

Effect of bioregion and breeder on 18-month weight

Results, presented in Table 5.7, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component of 18-month weight (18 MW_E) between some of the bioregions. There are no statistical differences in the 18 MW_E LSMs of the Central Bushveld and the Mesic Highveld Grassland. The proportion of variation in BW_E explained by bioregion is however very low (3%).

Results, presented in Table 5.6, reveal that the effect that the individual breeders have on 18 MW_E is also statistically highly significant ($p < 0.0001$). Breeder explains 24% of the variation in 18 MW_E. Breeder therefore has a much larger influence on 18 MW_E than bioregion (3%). The majority of the variation in 12 MW_E is therefore due to the influence of breeder, rather than bioregion.

Effect of bioregion and breeder on mature weight

Results, resented in Table 5.7, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component of mature weight (MW_E) of all the bioregions. The proportion of variation in MW_E explained by bioregion is, however, low (3%).

These results differ from those of a previous study done on Nellore cattle in Brazil. Differences in mature size was found by Souza *et al*. (2006), who investigated the mature size of Nellore cattle in two regions of Brazil by means of Richards growth equation. Results indicated that one region had significantly larger (69.05 kg) animals at maturity (A) than the other region.

Results, presented in Table 5.6, reveal that the effect that the individual breeders have on MW_E is also statistically highly significant ($p < 0.0001$). Breeder explains 26% of the variation in MW_E. Breeder therefore has a much larger influence on MW_E than bioregion (3%).

5.2.3. Effect of geographic location on the reproduction of Bonsmara cows

A cluster analysis was performed to investigate the effect that geographic location has on Bonsmara reproduction. Breeders were clustered by means of PROC Cluster according to their median herd RI. The dendogram shown in Figure 5.3 indicates that there are four clusters of breeders and two individual breeders with a distance of 0.5 between the cluster centroids.

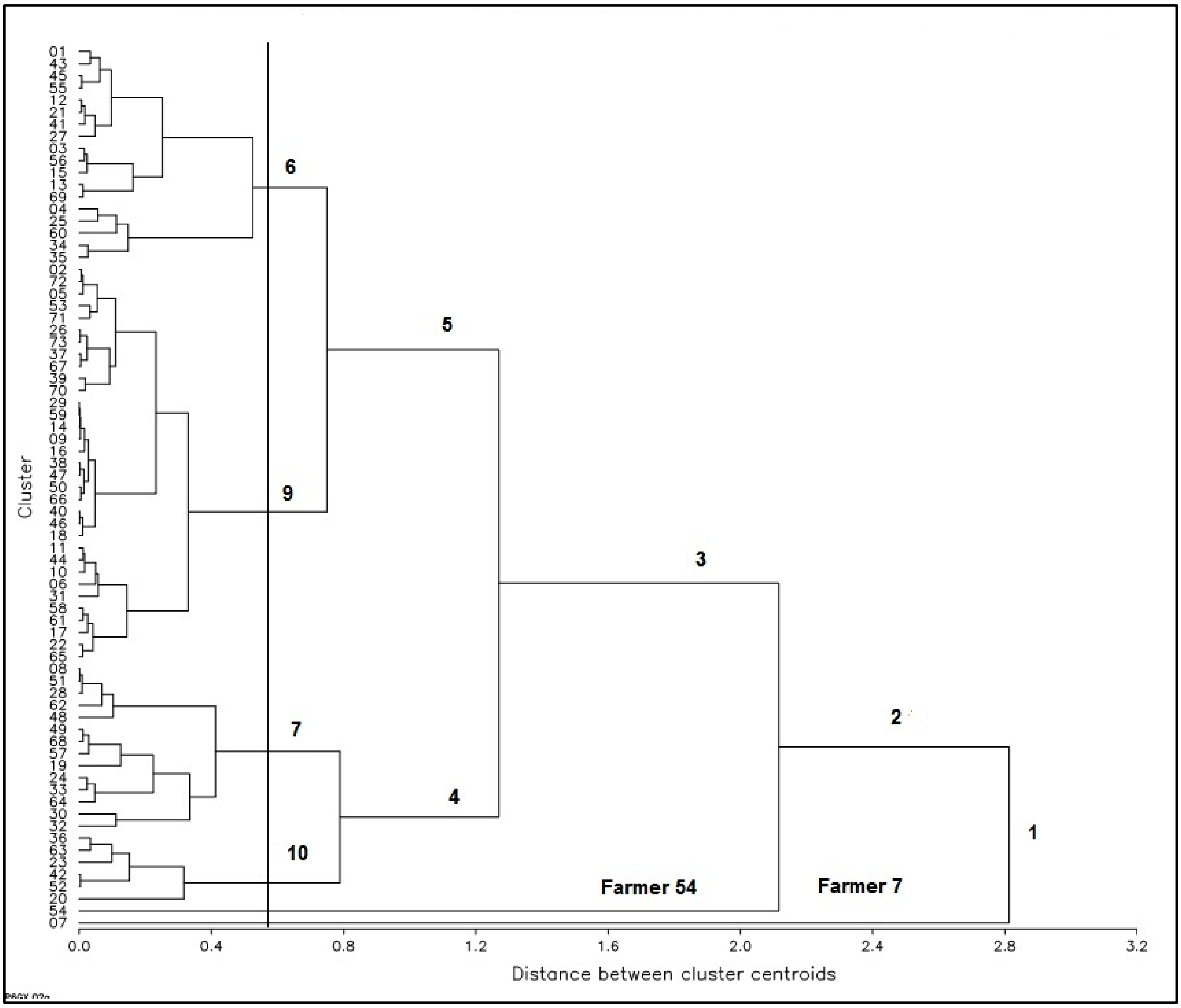

Figure 5.3 Clustering of breeders for the median of RI

Summary statistics regarding the number of animals and herds within a cluster, as well as the average median RI for the four clusters and two breeders, are presented in Table 5.9. In order to objectively assess the geographic distribution of herds located within cluster (cluster component herds) a summary of the number of cluster component herds per bioregion is given in Table 5.10. The geographic locations of the cluster component herds are shown in Figure 5.4.

Table 5.9 Summary of cluster contents for the median of RI

Cluster #	# Animals	# Herds	Median	Distance
Farmer 7	52	1	88	0
Cluster 10	750	6	95.8	0.32
Cluster 7	2072	14	100.7	0.41
Cluster 9	6628	33	105.9	0.33
Cluster 6	2986	18	110.6	0.53
Farmer 54	61	1	118.8	0

Table 5.10 Geographic location of cluster component herds per bioregion

	Eastern Kalahari Bushveld	Mesic Highveld Grassland	Dry Highveld Grassland	Central Bushveld	Total
Farmer 7	-	1	-	-	1
Cluster 10	-	3	-	3	6
Cluster 7	1	9	1	3	14
Cluster 9	7	9	11	6	33
Cluster 6	7	1	4	6	18
Farmer 54	-	-	1	-	1
AVG RI	106.8	102	106.2	103.5	104.6

Table 5.10 indicates that the Mesic Highveld Grassland bioregion, located in the eastern part of the country, has numerically the lowest average median RI (102). Three of the six herds contained in the cluster with the lowest RI median (Cluster 10) and nine of the 14 herds contained in the cluster with the second lowest RI median (Cluster 7) are located in the Mesic Highveld Grassland. Table 5.10 also indicates that the Central Bushveld, has the numerically second lowest average median RI (103.5). Three of the six herds located in the lowest RI median cluster (Cluster 10) are located in this bioregion.

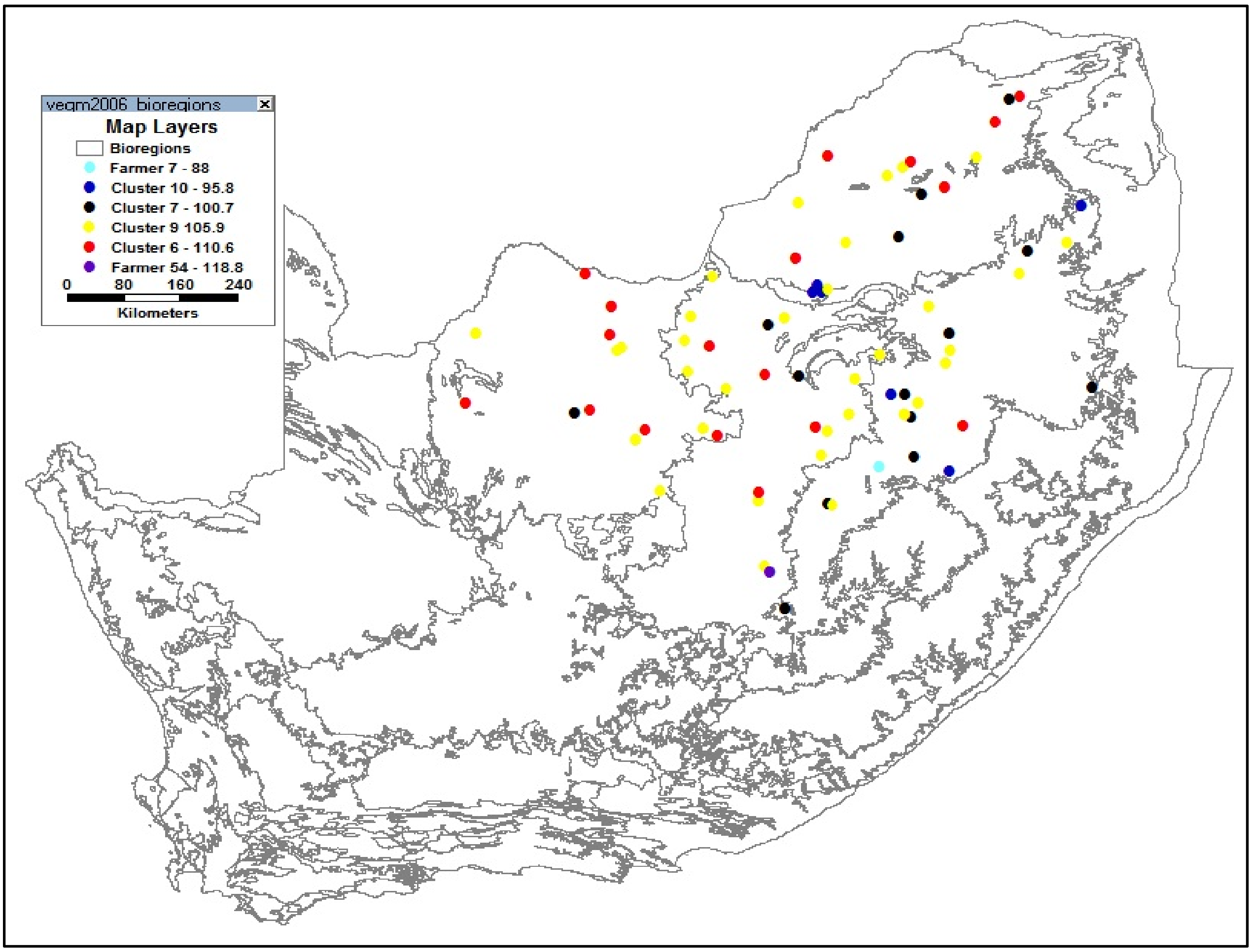

Figure 5.4 Geographic locations of the cluster component herds for RI

The geographic distribution of some of the herds that are grouped in clusters 10 and 7 (herds with lower RI medians) would seemingly support the belief that Bonsmara herds in the eastern parts of the country are less reproductive than those herds that are found in the western parts of the country. However, the distribution of the herds contained in the cluster with higher RI medians (Clusters 9 & 6) is geographically reasonably evenly distributed between the bioregion. An objective conclusion regarding the influence that geographic location has on Bonsmara reproduction can, therefore, not be made from the cluster analysis.

Table 5.11 LSM (LSM ± S.E) for reproduction traits per bioregion

Bioregion	AFC_E LSM	S.E	ICP_E LSM	S.E	RI LSM	S.E
Central Bushveld	980.3 [a]	2.34	420.5 [a]	1.51	103.5	0.18
Dry Highveld	958.0	2.29	412.7 [b]	1.44	106.2 [a]	0.17
Eastern Kalahari	935.1	1.86	418.1 [b, c]	1.15	106.8 [a]	0.14
Mesic Highveld	985.2 [a]	1.81	436.4 [a, c]	1.2	102.1	0.14

Least Square Means with same superscript do not differ statistically significantly ($p > 0.05$)

S.E	Standard Error
LSM	Least square means
Central Bushveld	Central Bushveld bioregion
Dry Highveld	Dry Highveld Grassland bioregion
Eastern Kalahari	Eastern Kalahari Bushveld bioregion
Mesic Highveld	Mesic Highveld Grassland bioregion
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period
RI	Reproduction index

5.2.4. Effect of production region on the reproduction traits of Bonsmara cows

One-way ANOVA was performed to investigate the effect that production region and breeder have on the reproduction efficiency of Bonsmara cows. Examples of ANOVA based on PROC GLM are given in Tables 5.4 and 5.5. The proportion of variation explained by bioregion and breeder (R^2) are presented in Table 5.6. The LSMs for the different reproduction traits are presented in Table 5.11. Summary statistics for the four bioregions are presented in Table 5.8.

Effect of bioregion and breeder on AFC

Results, presented in Table 5.11, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component of age at first calving (AFC_E) for some of the bioregions. There are no statistically significant differences between the Central Bushveld and the Mesic Highveld Grassland. The proportion of variation in BW_E explained by bioregion is however, low (3%). Ronchietto (1993), in the research previously referred to, found that there were statistically significant differences ($p < 0.01$) between the AFC of some of the agro-ecological regions.

Results, presented in Table 5.6, reveal that the effect that the individual breeders have on AFC_E are statistically significant ($p < 0.0001$). Breeder explains 23% of the variation in AFC_E. Breeder therefore has a much larger influence on AFC_E than bioregion (3%).

Effect of bioregion and breeder on ICP

Results, presented in Table 5.11, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of the environmental component inter-calving period (ICP_E) of some of the bioregions. There are no significant differences between the Central Bushveld and the Dry Highland Grassland, the Central Bushveld and the Eastern Kalahari Bushveld, and between the Eastern Kalahari Bushveld and the Dry Highland Grassland. The proportion of variation in ICP_E explained by bioregion was also very low (2%). Ronchietto (1993) in the research previously referred to found that there were statistically significant differences ($p < 0.01$) in ICP between some of the regions.

Results, presented in Table 5.6, reveal that the effect that the individual breeders have on ICP_E are statistically significant ($p < 0.0001$). Breeder explains 16% of the variation in ICP_E. Breeder therefore has a much larger influence on ICP_E than bioregion (2%).

Effect of bioregion and breeder on reproduction Index

Results, presented in Table 5.11, reveal that there are statistically significant ($p < 0.05$) differences between the LSMs of RI for some of the bioregions. There are no significant differences in RI between the Eastern Kalahari Bushveld and the Dry Highland Grassland. The proportion of variation in RI explained by bioregion is, however, low (5%).

Results, presented in Table 5.6, reveal that the effect that the individual breeders have on RI is statistically significant ($p < 0.0001$). Breeder explains 22% of the variation in RI. Breeder therefore has a much larger influence on RI than bioregion (5%).

5.3. CONCLUSIONS: EFFECT OF PRODUCTION REGION ON THE PRODUCTION EFFICIENCY OF BONSMARA COWS

There is a common perception amongst South African beef producers that cattle in the eastern, higher rainfall areas with its associated sourveld are smaller and less reproductive than those in the western, dry sweetveld areas of South Africa (J. v.d. Westhuizen. Personal Communication. SA Studbook. P.O. Box 270, Bloemfontein. 2011). The geographic distribution (Figures 5.2 & 5.4) of some of the herds with smaller less reproductive cows in the northern and eastern parts of the country seems to support the producers' perception.

However, when the influence of production region and breeder were statistically analysed by ANOVA it is clear that there is little statistical support for the producers' perceptions. Although there were statistically significant ($p < 0.05$) differences between bioregions for most of the production traits the actual biological differences were small. In large datasets it is often difficult to determine the biological versus the statistical importance of interactions, as some interactions will be statistically significant although the actual significance is of little or no biological importance (Burfening *et al.*, 1987). ANOVA results indicated that breeder in all cases had a much stronger ($p < 0.0001$) influence on the production traits than bioregion ($p < 0.05$). The proportion of variation in all the production traits was also explained to a much larger extent by breeder than by bioregion. The effect of the production region or environment on the efficiency of Bonsmara cows is therefore small when compared to the influence of individual breeders. The small influence of production region on the growth traits of Bonsmara cows is evident when illustrated graphically. Figure 5.5 give a graphic comparison between the LSM growth curves for each of the four bioregions.

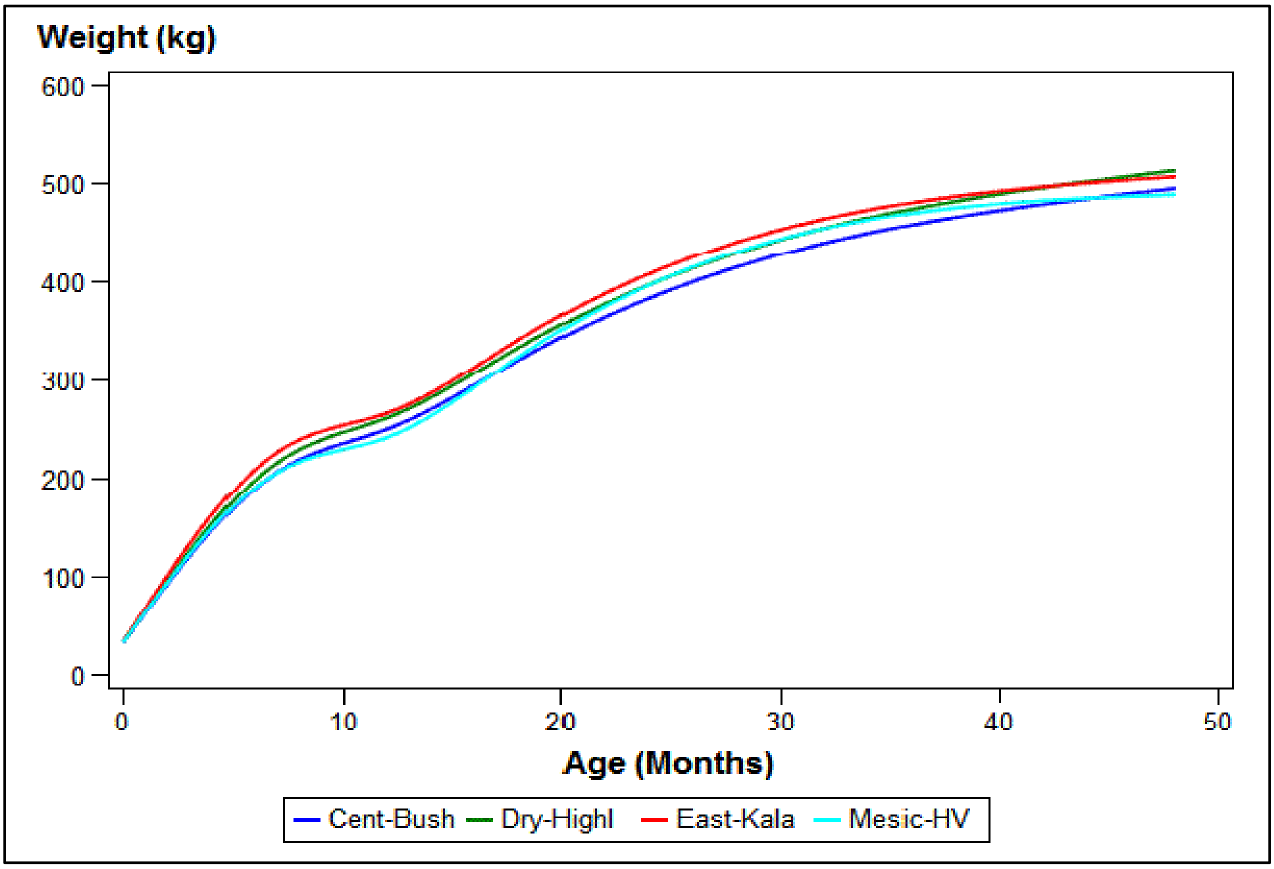

Figure 5.5 LSM for the growth characteristics of the different bioregions

Although little comparable research could be found for individual trait-environmental interactions for growth and size traits, the conclusions of this study are similar to those of other studies concerning birth weight (Burfening *et al.*, 1987; Botsime, 2005) and weaning weight (Cundiff *et al.*, 1966; Dooley *et al.* 1982; Leighton *et al.*, 1982; Burfening *et al.*, 1987; Ronchietto, 1993). No comparable results could be found for 12- and 18-month calf weights, while the results of this study differ from the results of Souza *et al*. (2006) regarding mature weight.

Comparison of some of the results to those from some of the previous research can not be compared because, with the exception of Ronchietto (1993) and Botsime (2005), none of the studies mentioned specifically investigated the effect of production region on cattle production. The regional classification systems used by those authors (Cundiff *et al*., 1966; Dooley *et al*. 1982; Leighton *et al*., 1982; Burfening *et al*., 1987) hardly took any bioclimatic information into account. This study also differs from previous studies as it takes the possible genetic differences between animals into account. The use of E-values (the exception being RI) removes the influence of additive genetic differences between animals. Previous studies presumably assumed that there were no genetic differences among animals.

The literature review showed that very little research has been done on the effect production region has on the reproductive ability of cattle. Research that used other reproductive measures than those used in this study also found little evidence of production region x reproduction interactions. Dooley *et al*. (1982), in the same research that was previously referred to, found that region had no effect on calving rate. Nqeno (2008), who investigated the effect that sweet- and sourveld-types had on the number of cows cycling in the Eastern Cape of South Africa, found no statistically significant differences in cycling rate between veld-types.

It can therefore be concluded, under the conditions of the study, that the influence of production region on Bonsmara cow efficiency is small, if anything at all, compared to the influence of the different farm environments as influenced by the breeders. It might be argued that the Bonsmara breeding philosophy might have contributed to these results. The Bonsmara breeding philosophy is based on the belief that cattle that are adapted to and are of optimal size for the environment they are expected to perform in will perform to their full genetic potential (Bonsma, 1983). Considerable emphasis has therefore historically been placed on selection for adaptability by Bonsmara breeders. Adapted cattle are, by definition, able to tolerate adverse environmental conditions while maintaining production efficiency (Bonsma, 1983). It can be hypothesised that the small influence of production region on Bonsmara cow efficiency may be due, in part, to the adaptive ability of the breed.

CHAPTER 6
EFFECT OF ENVIRONMENTAL CHARACTERISTICS ON THE PRODUCTION EFFICIENCY OF BONSMARA COWS

6.1. INTRODUCTION

The literature indicates that the major climatic processes that can influence livestock production are rainfall and temperature (Hafez, 1968). It has also been shown that the most important constraint to livestock production in extensive production systems is insufficient nutritional intake and specific nutrient deficiencies (De Waal, 1990). The nutritional value of the grazing is influenced by *inter alia* the soil nutrient status (McDonald et al., 2002). The effect of the environmental characteristics on the production efficiency of Bonsmara cows was, therefore, investigated by determining the influence of the major climatic and soil nutrient status indicators on Bonsmara production traits.

The following factors should be considered before the influence of environmental characteristics on traits recorded for Bonsmara cattle is discussed.

1. The environmental characteristics are not independent but are in some instances related. Rainfall is known to have an influence on pH, soil organic carbon (Brady & Weil, 2002a) and grazing capacity (Fourie, 1985). Soil pH has an influence on P and CEC (Brady & Weil, 2002a). Soil organic carbon has an influence on CEC (Brady & Weil, 2002b) and P (Whitehead, 2002).
2. The data source should also be considered. The production data used in this study are from well-established stud herds. It can be assumed that the breeders use feed and lick supplementation programmes to increase the nutrient intake and supplement deficiencies in their grazing (De Waal, 1990). The supplementing programmes may have a confounding influence on certain interactions.
3. The influence of the environment on specific production traits should also be considered in relation to the growth curve of the study population. The growth curve is presented in Figure 6.1.
4. The 1:250 000 scale maps of AGIS, from which the environmental characteristic data were sourced, has limited accuracy for farm level-use (Collet, 2008b). Environmental characteristic data are therefore not as accurate as desired.

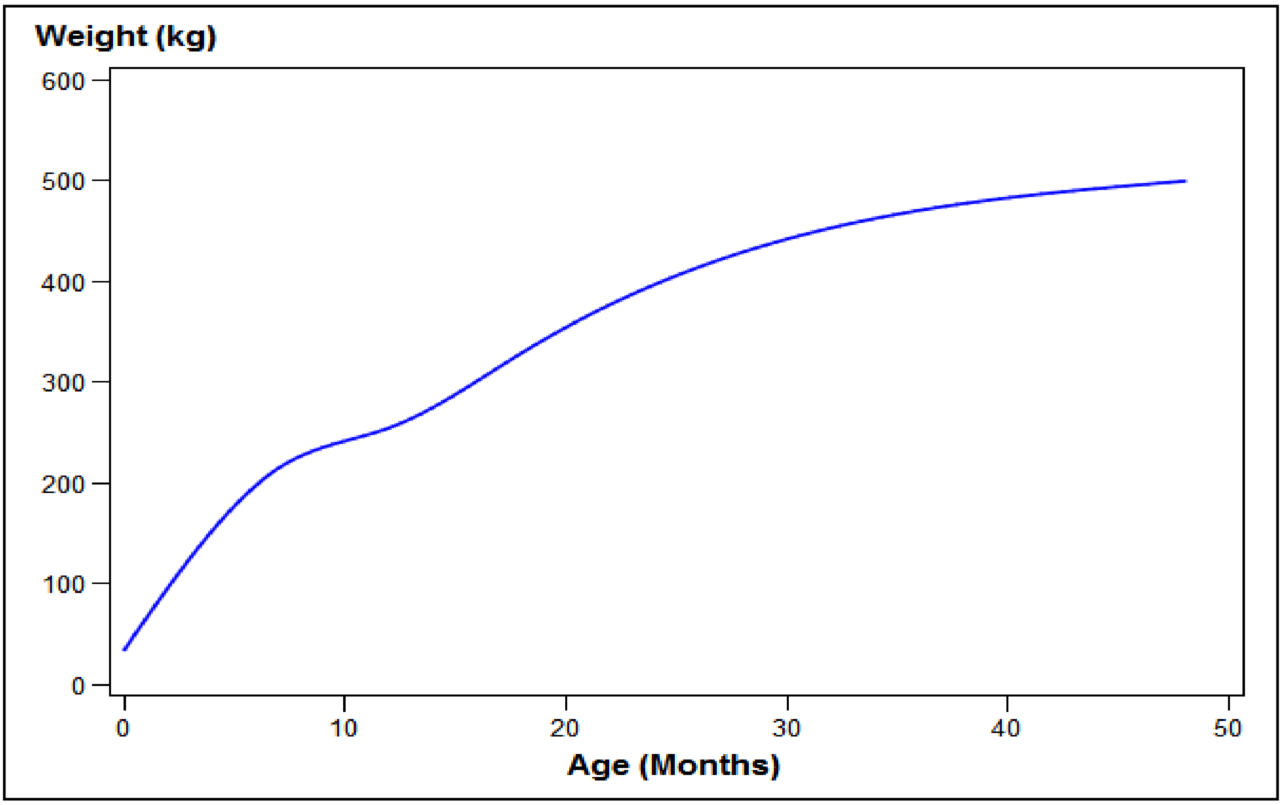

Figure 6.1 Growth curve for the 12 549 Bonsmara cows included in the study

6.2. RESULTS & DISCUSSION

6.2.1. Combined environmental effects on production traits of Bonsmara cattle

The relationship between the environmental characteristics (temperature, rainfall, CEC, soil pH, soil organic carbon, soil P, and grazing capacity) and the production traits were determined by PROC REG using the stepwise option. Results of PROC REG are shown in Table 6.1. Linear regressive models reveal that the combined environmental characteristics have a statistically significant ($p < 0.0001$) influence on the production traits of Bonsmara cows. The proportion of variation explained by the combined environment was however, not large. Unfortunately, very few comparable research results could be found.

Combined environmental effect on BW_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on BW_E. The combined environmental effects, however, explain only a small (4%) proportion of variation in BW_E. The small influence (4%) that environmental characteristics have on BW_E is possibly due to the buffering effect of the uterine environment. The uterine environment is sensitive to the effects of the maternal dietary intake (Funston *et al*., 2010), global nutrient supply (Larson *et al*., 2009) and temperature (Bernabuccil *et al*., 2010). The possibility of manipulating the birth weight of Bonsmara calves through the manipulation of their production environment is therefore limited. However, an opposing opinion could be that the environment will also have an effect on the dam in this regard.

Combined environmental effect on WW_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on WW_E. The combined environment explains a large (9%) proportion of the variation in WW_E. The weaning weight of a calf is determined by the calf's own additive genetic merit for growth as well as the maternal environment created by the dam (Deese & Koger, 1967; Van Niekerk *et al*., 2004). A major component of the dam's maternal environment is the nutrition that the calf receives through milk intake (Clutter *et al*., 1987). A positive relationship exists between the dam's breeding values for milk, her milk production and the weaning weight of the calf (Marston *et al*., 1982). The milk yield of a cow is, therefore, the main determinant of maternal effects on the growth of beef calves (Rutledge *et al*., 1971; Clutter *et al*., 1987; Meyer *et al*., 1994). The milk yield of a cow is partially determined by the quality of her forage (Grings *et al*., 1996). Forage quality can therefore affect the growth rate of a calf through effects on the milk yield of the dam and the quality of the forage portion of the calf's diet (Grings *et al*., 1996). The environmental influence on the weaning weight of Bonsmara calves is therefore probably largely indirect, through the effect of environmental characteristics on the forage quality and quantity and, therefore, the nutritional intake of the grazing cow and her calf.

Combined environmental effect on 12 MW_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on 12 MW_E. The combined environment explains a large (10%) proportion of the variation in 12 MW_E. The growth curve of the Bonsmara cows (Figure 6.1) indicates that the Bonsmara heifers were subjected to wean stress from 7 to 12 months. The wean stress is probably due to the management practices employed by breeders. The majority of South African beef calves are born during the summer and are weaned during early winter. The weaned calves are therefore dependent on winter forage for their maintenance and growth requirements. The decline in growth rate (wean stress) is therefore probably caused by the removal of the maternal environment after wean and the less nutritious forage of the winter months. The results indicate that the environment has a larger (10%) influence on 12 MW_E than on WW_E (9%), indicating the larger exposure of the yearling calf to the environment after the maternal environment is removed after weaning.

Combined environmental effect on 18 MW_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on 18 MW_E. The combined environment explains some (5%) of the variation in 18 MW_E. The growth curve, indicated in Figure 6.1, shows that a period of compensatory growth occurs after the calves reach yearling age. The compensatory growth seen between 12 and 18 months of age are probably due to the seasonal changes and a response to lick supplementation. Calves born in summer reach yearling age at the onset of spring and graze on summer pastures during the subsequent months. Breeders often provide nutritional supplementation during this period to ensure that the heifers reach mating weight at 18 months of age. The smaller environmental effect (5%), than wean and yearling age, seen at 18-month age is possibly a reflection of the less stressful season (summer).

Combined environmental effect on MW_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on MW_E. The combined environment explains some (7%) of the variation in MW_E. Mature cows have been exposed to the environment for a longer period and it is expected that the environmental influence on mature weight should be visible. The large (7%) effect that the combined environment has on MW_E is an indication that the production environment does have an effect on the mature weight of Bonsmara cows.

Combined environmental effect on AFC_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on AFC _E. The combined environment explains some (7%) of the variation in AFC_E. It was indicated by Rust & Groeneveld (2001) that in the South African context the management decisions of the breeders have a larger influence on the AFC of heifers than genetic merit. Most Bonsmara breeders breed their heifers when they reach target breeding weight. The environmental effect on AFC could therefore be due to a confounding effect of the environment on growth rate of the heifer calves. The large influence of the environment on AFC is an indication of the extent to which AFC can be improved through the manipulation of the environment.

Combined environmental effect on ICP_E

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on ICP_E. The combined environment explains some (5%) of the variation in ICP_E. ICP is an aggregate reproductive trait that is composed of more than one reproductive event. The literature shows that numerous factors can have an effect on the ICP of a cow (Montiel & Ahuja, 2005). Nutrition is, however, often regarded as being the most important contributing factor (Montiel & Ahuja, 2005).

Combined environmental effect on RI

Results indicate that the combined environment had a statistically significant ($p < 0.0001$) effect on the RI. The combined environment explains a (10%) proportion of the variation in RI. RI is a composite reproduction index and is composed of both AFC and ICP. The influence of the combined environment on RI is larger than the influence of the environment on AFC_E and ICP_E. This is probably due to the compounding effect of similar environmental characteristics that have a similar influence on both AFC and ICP. The large influence of the environment on RI is an indication of the extent to which RI can be improved by the manipulation of the environment.

Table 6.1 Stepwise regression results indicating the environmental characteristic effects on production traits

Traits	**Intercept**	**Model**														**M-R²**	**C(p)**
		T		**R**		**P**		**pH**		**SOC**		**CEC**		**GC**			
		P-E	**P-R²**	**P-E**	**P-R²**	**P-E**	**P-R²**	**P-E**	**P-R²**	**P-E**	**P-R²**	**P-E**	**P-R²**	**P-E**	**P-R²**		
BW_E	39.97	0.09	0.02	-0.01	< 0.01	-0.20	< 0.01	-	-	0.30	< 0.01	-0.04	< 0.01	-0.20	< 0.01	0.04	6.95
WW_E	261.43	-0.78	< 0.01	-0.07	0.08	-	-	2.69	< 0.01	-		-0.41	< 0.01	-	-	0.09	4.93
12 MW_E	363.88	-1.72	< 0.01	-0.08	0.09	-	-	-3.12	< 0.01	-14.10	< 0.01	0.72	< 0.01	0.55	< 0.01	0.10	6.02
18 MW_E	401.58	-1.51	< 0.01	-0.06	0.04	-	-	1.99	< 0.01	-11.98	< 0.01	-	-	-	-	0.05	4.79
MW_E	699.41	-1.33	< 0.01	-0.20	0.02	-4.30	0.01	4.18	< 0.01	-14.83	0.03	-	-	-4.56	0.01	0.07	6.01
AFC_E	219.54	15.29	0.01	0.34	0.02	12.72	0.01	-	-	45.11	0.03	2.85	< 0.01	1.83	< 0.01	0.07	6.77
ICP_E	120.68	2.01	< 0.01	0.30	0.01	4.75	< 0.01	-	-	-16.65	0.01	2.81	0.01	4.97	0.01	0.05	6.36
RI	159.89	-0.52	0.01	-0.05	0.04	-1.29	0.02	0.54	< 0.01	1.71	< 0.01	-0.40	0.01	-0.76	0.02	0.10	8.00

All models are statistically highly significant with $p < 0.0001$

P-E	Parameter Estimate
M-R²	Model-R²
P-R²	Partial-R²
T	Temperature
R	Rainfall
P	Phosphorus
SOC	Soil organic carbon
CEC	Cation exchange capacity
GC	Grazing capacity
BW_E	Environmental component of birth weight
WW_E	Environmental component of wean weight
12 MW_E	Environmental component of 12-month weight
18 MW_E	Environmental component of 18-month weight
MW_E	Environmental component of mature weight
AFC_E	Environmental component of age at first calving
ICP_E	Environmental component of inter-calving period
RI	Reproduction index

6.2.2. Individual environmental effects on production traits of Bonsmara cattle

The regression analysis (PROC REG) that was used for the previous analysis and that are presented in Table 6.1, was used to compare the direction and size of the contribution of environmental characteristics across models. Coefficients from different linear models are not comparable and only the tendencies will be discussed.

Temperature

Across-model comparisons revealed that temperature, with the exception of BW_E, had a statistically significant ($p < 0.0001$) negative correlation with all the growth, size and reproduction traits. This result is expected in the light of the description of the effect of heat stress by authors like Bonsma, (1983) and Du Preez *et al.*, (1992). Heat stress occurs when the environmental variables such as ambient temperature, humidity, air movement and solar radiation combine to reach values that surpass the upper limit of the thermo neutral zone (Bernabuccil *et al*., 2010). Heat-stressed animals tend to decrease their feed intake and rumination time, resulting in a decrease in nutrient intake (Collier *et al*., 2005) that results in a negative energy balance (Bernabuccil *et al.*, 2010). Heat stress also results in an altered endocrine status that increases maintenance requirement (Collier *et al*., 2005). The negative relationship between temperature and the growth and size traits are therefore due to the depressing influence that high environmental temperatures have on the energy status of the cows. The biological mechanisms responsible for the negative influence that heat stress has on female reproduction are, however, not yet completely understood (Rhoads *et al*., 2009). Although the influence of temperature on the production traits is statistically significant ($p < 0.0001$) the actual influence is small (partial R^2 values ≤ 0.01). This study found that that temperature has a statistically significant but biological small impact on the reproductive ability of Bonsmara cows. It is therefore debatable if temperature has a significant biological impact on the production efficiency of the Bonsmara cows included in the study. The study population however only included reproductive, and per implication, adapted animals. The dataset is therefore biased.

It was reported by Amundson *et al*. (2005) that the conception rates of Bos Taurus cattle declined in temperatures above 23.4 C. This study however found no strong relationship between temperature and Bonsmara reproduction traits. The results, however, indicate an unexpected statistically significant ($p < 0.0001$) positive relationship between temperature and BW_E. Heat stress is known to decrease foetal growth (Bernabuccil *et al*., 2010). It is therefore possible that the Bonsmara cows included in the study are well within their zone of adaptability and that ambient temperature has no negative influence on BW_E in this study.

Rainfall

The results revealed that rainfall has a statistically significant ($p < 0.0001$) negative relationship with all the growth, size and reproduction traits. Rainfall is the environmental characteristic with numerically the largest influence on production efficiency, as it makes the largest numerical partial contribution to WW_E, 12 MW_E, 18 MW_E and RI. The relationship found between rainfall and growth is similar to that of Neser *et al*. (2008) who found that rainfall explained 10% of the weaning weight of Bonsmara weaner calves. Fynn & O'Conner (2000) also found a curvilinear relationship between rainfall and cattle production.

It is accepted that rainfall has a large influence on the quantity and quality of forage (Tainton & Hardy, 1999; Fynn & O'Conner, 2000). The negative relationship between rainfall and the production traits can be explained based on the traditional South African sweet-, mixed-, and sourveld classification system. The classification system refers to the period of the year in which the natural grazing can sustain animal production without supplementation (Tainton, 1999). Sweetveld is the most nutritious throughout the year and generally occurs in areas that receive 200-500 mm of rainfall (Van Rooyen, 2002). Sourveld become unacceptable and less nutritious after maturity and generally occurs in areas that receive at least 650 mm (Van Rooyen, 2002). There is therefore a general tendency for nutritional value of South Africa's forage to decline during winter in higher rainfall areas. The negative relationship between rainfall and Bonsmara production traits is consequently probably due to the influence that rainfall has on the nutritional value of the forage and therefore nutrient intake.

Rainfall has also been shown to have an influence on other environmental characteristics such as pH, soil organic carbon (Brady & Weil, 2002b) and grazing capacity (Fourie, 1985). The influence of rainfall on these environmental characteristics could therefore influence the results of the effect that these characteristics have on Bonsmara production.

Soil P

Results revealed that soil P has a statistically significant ($p < 0.0001$) negative relationship with BW_E, MW_E and the reproduction traits. The results are surprising as they indicate that increased P soil levels decrease BW_E, MW_E and the reproductive efficiency of Bonsmara cows. It is well known that P-deficiency is associated with subnormal growth and fertility (McDonald *et al*., 2002) and numerous studies have shown that P-supplementation has a major positive impact on the growth, size (Read *et al.*, 1986; De Waal *et al*, 1996; De Brouwer *et al*., 2000) and reproduction (Read *et al.*, 1986; De Waal *et al*, 1996; Orsmond, 2007) of beef cattle in South Africa. Large areas of South Africa are deficient in P (Du Toit *et al*., 1940; Meissner, 1999). A positive relationship between P and Bonsmara production traits is therefore expected. P-supplementation is, however, widely provided for grazing cattle in South Africa (De Waal *et al*, 1990). The unexpected result may be due to the effective P-supplementation programmes followed by breeders in P-deficient areas and an indication that breeders located in higher P areas provide less P-supplementation.

Soil pH

Results revealed that pH has a statistically significant ($p < 0.0001$) positive relationship with WW_E, 18 MW_E, MW_E and RI. An unexpected negative relationship was found between pH and 12 MW_E. The relationship is, however, weak and the partial contribution small. The growth curve indicates that Bonsmara heifers suffer from wean shock from 7 to 12 months. This unexpected relationship is therefore possibly due to a physiological process that accompanies weaning shock. The positive relationship therefore indicates that the more acidic soils (lower pH) have a negative influence on most of the production traits. The relationship between soil pH and the Bonsmara production traits is, however, weak (all partial $R^2 < 0.01$) and therefore not necessarily biologically significant. Soils with a lower pH (more acid) are generally associated with higher rainfall areas (Brady & Weil, 2002a). It was previously shown that rainfall also has a negative relationship with the production traits. The relationship between soil pH and Bonsmara production traits may therefore be due to the indirect influence of rainfall.

Soil organic carbon

Results revealed that there are a statistically significant ($p < 0.0001$) negative relationship between soil organic carbon and 12 MW_E, 18 MW_E and MW_E, while there is a statistically significant ($p < 0.0001$) positive correlation with soil organic carbon content and BW_E. There is also a large negative relationship between AFC_E and a positive relationship with RI and ICP_E. The influence of soil organic carbon on the production traits is therefore not clear.

CEC

Results revealed that CEC has a statistically significant ($p < 0.0001$) negative relationship with BW_E, WW_E and a positive relationship with 12 MW_E. The contribution of CEC to the growth is small (partial $R^2 < 0.01$). Bonsmara growth is, therefore, hardly influenced by CEC. The small (partial $R^2 < 0.01$) negative relationship between CEC and Bonsmara reproduction traits is, however, interesting as soil with high CEC has a greater ability to retain its nutrient cations and are hence more fertile (Whitehead, 2000). The result is therefore unexpected as it would be expected that more fertile soils would have a positive relationship with reproduction traits due to the associated higher forage quality. The influence of CEC on the production traits is therefore not clear.

Grazing capacity

Results revealed that grazing capacity has a statistically significant ($p < 0.0001$) negative correlation with BW_E, 12 MW_E and MW_E, while there is a statistically significant ($p < 0.0001$) positive correlation between grazing capacity and 12 MW_E. The positive relationship between grazing capacity and 12 MW_E might be from the wean shock effect. Grazing capacity is also negatively correlated with Bonsmara reproduction traits. Grazing capacity is, however, influenced by rainfall (Fourie, 1985), and the relationship between grazing capacity and growth and size traits may therefore be influenced by the influence of rainfall on the production traits. The influence of grazing capacity on the production traits is therefore not clear.

6.3. CONCLUSIONS: EFFECT OF ENVIRONMENTAL CHARACTERISTICS ON THE PRODUCTION EFFICIENCY OF BONSMARA COWS

Results from this study are remarkably consistent with the known environmental effects on livestock production, given the data source and experimental design. The quantifiable nature of the environment influence on extensive beef production is highlighted and areas where management will increase the production efficiency of Bonsmara cows are identified.

A few of the individual environmental characteristic interactions investigated in this study were found to be contradictory to the known relationships. A probable cause could, however, be identified in most cases. Some of the results from the investigation into the effect of soil and grazing characteristics on Bonsmara production efficiency were not always clear. The results might indicate that there is little interaction between Bonsmara cows and the soil- and grazing characteristics. It was indicated that the AGIS- (Collet, 2008b) and grazing capacity map (P. Avenant. Personal Communication. DAFF. Cnr Annie Botha and Union Street, Riviera, Pretoria. 2010) are not necessarily accurate enough for farm level use. The lack of relationship between the production traits of Bonsmara cows and the soil- and grazing characteristics might therefore be due to inaccurate environmental characteristic data. Alternatively, it is possible that the lack of interaction between the Bonsmara production traits and soil and grazing characteristics might also be due to efficient lick and feed supplementation programmes. That would indicate that efficient lick and feed supplementation programmes are able to mitigate any negative environmental influences regarding soil and nutritional interactions.

Individual environmental effects on Bonsmara production traits

The results indicate that rainfall and temperature were the environmental characteristics that had the most pronounced influence on Bonsmara production traits. Rainfall was shown to be the environmental characteristic with the largest influence on the production efficiency of Bonsmara cows. Bonsmara heifer weights were influenced to the largest extend at wean- and yearling age by rainfall. It is postulated that the negative relationship between the growth, size and reproduction traits and rainfall is due to the influence that rainfall has on the forage quantity and quality and, therefore, the nutrient intake of extensively managed Bonsmara cows. Temperature was also found to have an influence on the production efficiency of Bonsmara cows. Temperature was shown to have a negative relationship (with the exception of birth weight) on the growth, size and reproduction traits of Bonsmara cows. The negative relationship implies that Bonsmara cows are, to a lesser extent, susceptible and negatively influenced by heat stress. Recent EBV trends (shown in Figure 1.3) however show that remarkable progress has been made in growth potential of the Bonsmara breed. Concerns have been raised regarding the negative influence that such an increase in growth potential may have on adaptability (Green *et al*., 2007). These concerns are, however, not always supported by experimental results (Prayaga & Henshall, 2005). It is therefore possible, but debatable, if the improvement in growth potential would have had a negative influence on the adaptability of the Bonsmara breed. The influence of temperature on growth, size and reproduction traits is, although statistically significant, fairly low. It is therefore questionable whether the negative influence is biologically relevant. The weak relationship might even suggest that Bonsmara cows are well adapted to the main South African beef production regions, as a stronger relationship is expected between temperature and the growth and reproduction traits in un-adapted cattle.

Combined environmental effects on Bonsmara production traits

When the influence of the combined environment on the growth curve of the Bonsmara cows was investigated it was evident that the influence of the environment on growth changes through the phases of the growth curve. The change of influence on growth is due to the interrelationships between the individual's animal’s inherent impulse to grow and mature and the environment in which these impulses are expressed (Fritzhugh, 1967). A graphical presentation of the proportion of variation explained by the combined environment is given in Figure 6.2. The proportion of variation explained by the combined environment in a specific trait is an indication to what extent the environment influences that trait. By implication this also means that the larger the variation, the larger the opportunity to improve cow efficiency through management practices.

The h^2 of a trait (Tables 2.2 and 2.3) gives an indication of the relative importance of environmental effects (E) on a trait. In this study the E component were therefore already accounted for. The results therefore indicate what part of the E is explained by the individual environmental characteristics tested.

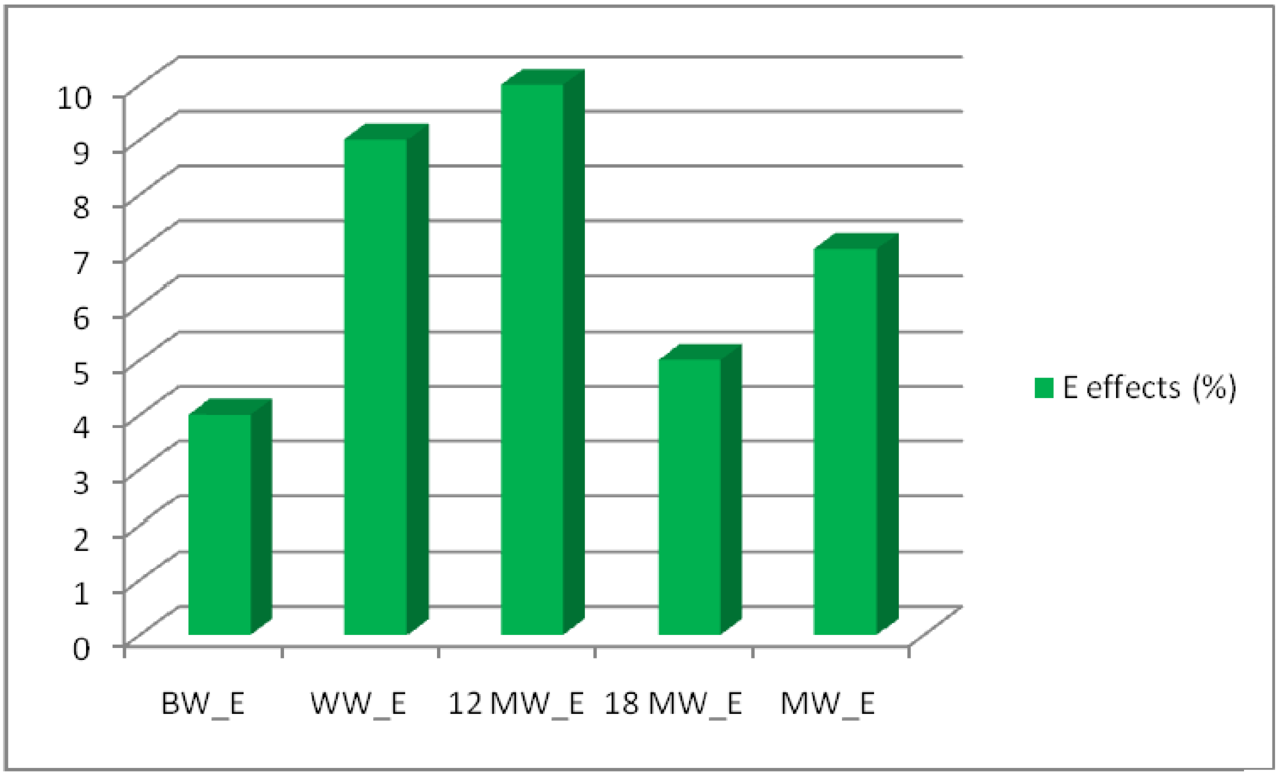

Figure 6.2 Environmental effect on Bonsmara growth curve

The results indicate that the environment’s effect on birth weight is small (4%). The buffering effect of the uterine environment therefore shields the neonatal calf from the influence of the environment. The environment, however, has a numerically much larger influence on the weaning- (9%) and yearling weight (10%) of Bonsmara heifers. It is argued that the influence is partly due to common management practices employed by breeders. Summer calves are weaned during early winter and consequently raised on winter grazing. Rainfall was shown to have a large negative relationship on heifer weight at wean and yearling age due to its influence on the quality of the grazing. These results indicate that nutritional supplementation from prior to wean till post yearling age has the greatest potential to improve the production efficiency of extensively managed Bonsmara cows in the higher rainfall (sourveld) areas of South Africa. The environment has a numerically smaller (5%) influence on the 18-month weight of heifer calves. The lower environmental influence is probably caused by the influence of season (summer) and the management procedures employed by breeders to get their heifers into condition for breeding at 18 months. The environments influence on Bonsmara cow size that is surprisingly large (7%). This is however expected, as the mature cows have been exposed to their prevailing production environment for a far longer period.

The combined environment has a significant influence on the reproduction efficiency of Bonsmara cows. It is argued that the influence of the environment on AFC (7%) is largely due to the indirect influence that early growth has on AFC. Heifers are generally mated by weight, rather than age. It was shown that rainfall had a statistically significant negative influence on AFC. The influence of rainfall on AFC is therefore probably due to nutrition and, therefore, growth interaction. The combined environment also has a substantial influence (5%) on ICP. ICP is a complex trait that is influenced by numerous intrinsic and extrinsic factors. The results are not clear on the underlying causal interactions. The effect of the combined environment on RI is larger (10%) than that of AFC and ICP. The RI of a cow is a combination of her AFC and ICP. The larger influence would probably be due to the same environmental characteristics that have an independent influence on both AFC and ICP and that result in a larger combined influence.

CHAPTER 7
EFFECT OF MATURE SIZE ON THE REPRODUCTION EFFICIENCY OF BONSMARA COWS

7.1. INTRODUCTION

There is general consensus in the literature that optimal cow size for reproduction efficiency will be different for each breed and type (Brown, *et al*., 1989; Johnson, *et al*., 1990; Taylor *et al*,. 2006) and will vary between production systems and environments (Morris & Wilton, 1976; Anderson, 1978; Dickerson, 1978; Fitzhugh, 1978). Optimal weights for Bonsmara breeding females was suggested by MacGregor & Swanepoel (1992). It was shown that the majority of South Africa's rangeland is arid or semi-arid (Schulze, 1997) and nutritionally limited (De Waal, 1990). Results from the study of Jenkins & Ferrell (1994) indicates that cattle with moderate maintenance requirement and production potential are more efficient when nutrient availability is limited because their reproduction rate will be less affected than cows with a higher maintenance requirement and production potential. This view is supported by several authors (Dickerson, 1978; Buttram & Willham, 1986; Solis *et al*., 1988; Taylor, 2006). It is therefore generally expected that smaller cows should be reproductively more efficient in the climatically challenging South African production environment.

7.2. RESULTS & DISCUSSION

The relationship between Bonsmara mature cow weight (MW_E) and reproduction efficiency (RI) was investigated by means of regression analysis (PROC REG) to determine the linear relationship between and across production region. A summary of all linear regressions is presented in Table 7.1.

Table 7.1 Summary of linear regressions between Bonsmara cow MW_E and RI

			LSM	
Region	**Regression model**	**R^2**	**RI**	**MW_E**
Across regions	RI = 0.026(MW_E) + 91.47	0.025	104.6	499.5
Central Bushveld	RI = 0.032(MW_E) + 87.72	0.033	103.5	494.3
Dry Highveld Grassland	-	-	106.2	512.3
Eastern Kalahari Bushveld	RI = 0.013(MW_E) + 100.41	0.0066	106.8	506.3
Mesic Highveld Grassland	RI = 0.031(MW_E) + 100.41	0.035	102.0	488.1

7.2.1. Relationship between cow size and reproduction efficiency across production regions

The results reveal that there is a positive linear relationship between MW_E and RI. The relationship is statistically significant ($p < 0.0001$) and is described as RI = 0.026(MW_E) + 91.47. The proportion of variation in RI explained by MW_E is, however, very low ($R^2 = 0.025$). Linear regression output is shown in Figure 7.1.

The positive relationship between mature weight and reproduction indicates that there is a tendency for larger Bonsmara cows to be more reproductive than small Bonsmara cows. Although the fit of the linear regression line is poor ($R^2 = 0.025$), it is expected, as mature cow size has no direct influence on the reproduction ability of the cow. The effect of mature cow size on reproduction would be indirect through the effect that cow size has on the animal's response to the prevailing climate and available food resources (Arango & Van Fleck, 2002).

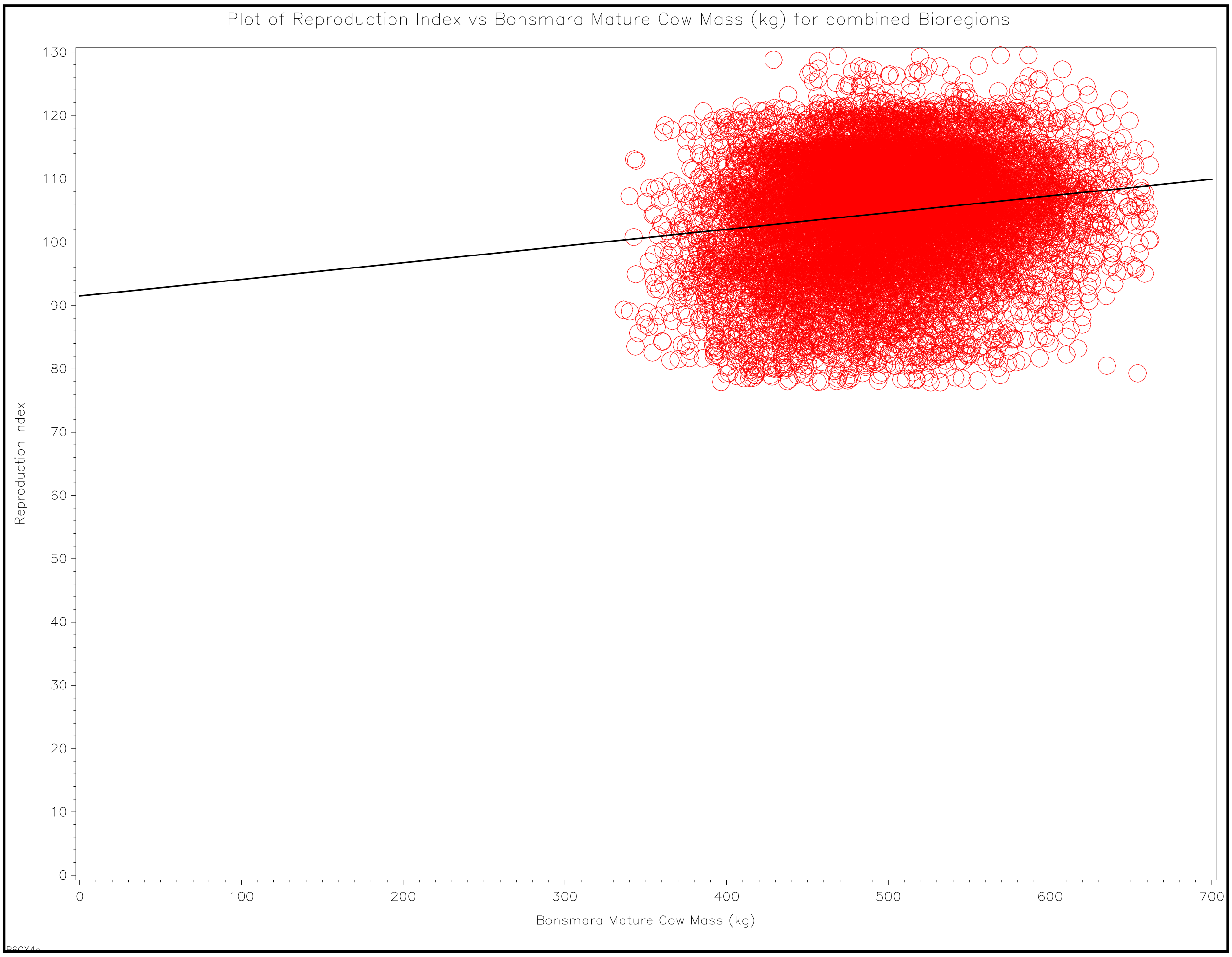

Figure 7.1 Linear relationship between Bonsmara cow MW_E and RI across production regions

A number of researchers have found a similar positive relationship between cow size and reproduction. Steenkamp & Van der Horst (1974) report that large- and medium-framed Afrikaner cows had higher reproductive rates than small-framed Afrikaner cows in an arid part of Zimbabwe. Meaker (1975) reports a similar positive correlation between Afrikaner mature cow weight and re-conception in the then Northern Natal region of South Africa. Macgregor & Swanepoel (1992) report a positive relationship between body weight and the re-conception rate of Bonsmara cows in the Eastern Cape. These authors, however, indicate that obesity was a cause of failed reproduction in mature cows.

A large number of conflicting reports also exist. In a large, long-term study Lademan & Schoeman (1994) investigated the factors that influence the re-conception rate of four purebred and three crossbred beef breeds in the arid Northern parts of South Africa. These authors concluded that cow body mass has no significant effect on the re-calving rate of beef cows. Results indicating a negative relationship between cow size and reproduction have also been published. Luna-Nevarez (2010) found a negative correlation between cow size and pregnancy rates in Brangus cattle in the semi-desert of New-Mexico. At Matopos, an arid region of Zimbabwe, it was found that the most fertile cattle breed (Mashona) also had the lowest average mature body weight (Moyo *et al*, 1996). In a similar study that was performed in South Africa, the smaller-framed breed Nguni breed was also found to be the most reproductive (Du Plessis *et al.*, 2006). It was, however, noted by Du Plessis et al. (2006) that in studies performed between breeds, the inherent reproductive ability of the breeds may have a larger influence on the expression of reproduction rate than frame size. In a study performed on Santa Gertrudis cows in arid North Eastern Namibia it was found that that small- and medium-framed cows had a higher reproduction rate than large cows (Taylor, 2006). It was similarly reported by Vargas *et al*. (1999) that selection for larger Brahman cattle resulted in reduced fertility on planted pastures in sub-tropical Florida, USA.

It is evident that there is no consensuses in the literature regarding the influence that mature cow size has on the reproductive ability of beef cows. In the study of Lademan & Schoeman (1994) it was concluded that cow size should not restrict the reproduction ability of extensively managed beef cows, when they are managed under favourable conditions. The positive relationship that was found between mature cow size and reproduction is therefore, an indication that the Bonsmara cows included in this study are managed under favourable conditions for the breed.

7.2.2. Relationship between cow size and reproduction efficiency within production region

Cow size and reproduction in the Central Bushveld

Results reveal that there is a statistically significant positive relationship between MW_E and RI in the Central Bushveld. The relationship is statistically significant ($p < 0.0001$) and is described as RI = 0.032(MW_E) + 87.72. The proportion of variation in RI explained by MW_E is, however, small (R^2 = 0.033). Linear regression output is shown in Figure 7.2.

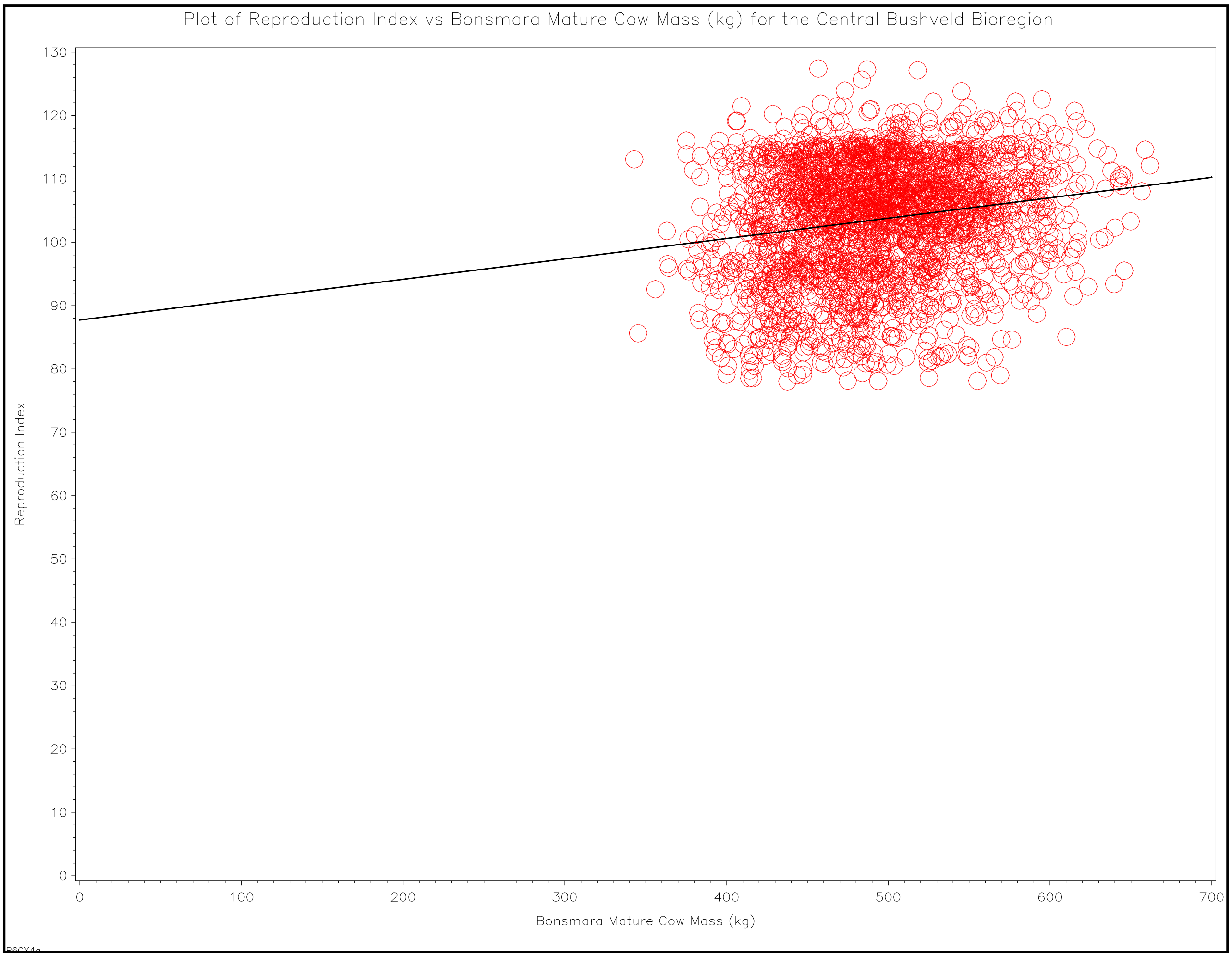

Figure 7.2 Linear relationship between Bonsmara cow MW_E and RI in the Central Bushveld

The positive relationship indicates that there is a tendency in the Central Bushveld for larger cows to be more reproductive than smaller cows. Previous results indicate that Central Bushveld mean for MW_E is 494.3 kg, which is slightly lower than the Bonsmara mean MW_E of 499.5 kg. The RI mean of the Central Bushveld is 103.5, which is also less than the breed RI mean of 104.6. Selection for larger than current average sized Bonsmara cows in the Central Bushveld should, therefore, lead to improved reproduction efficiency in the Central Bushveld.

Cow size and reproduction in the Dry Highveld Grassland

Linear regression results are indicated in Figure 7.3. The results reveal that there is no statistical relationship between MW_E and RI in the Dry Highland Grassland.

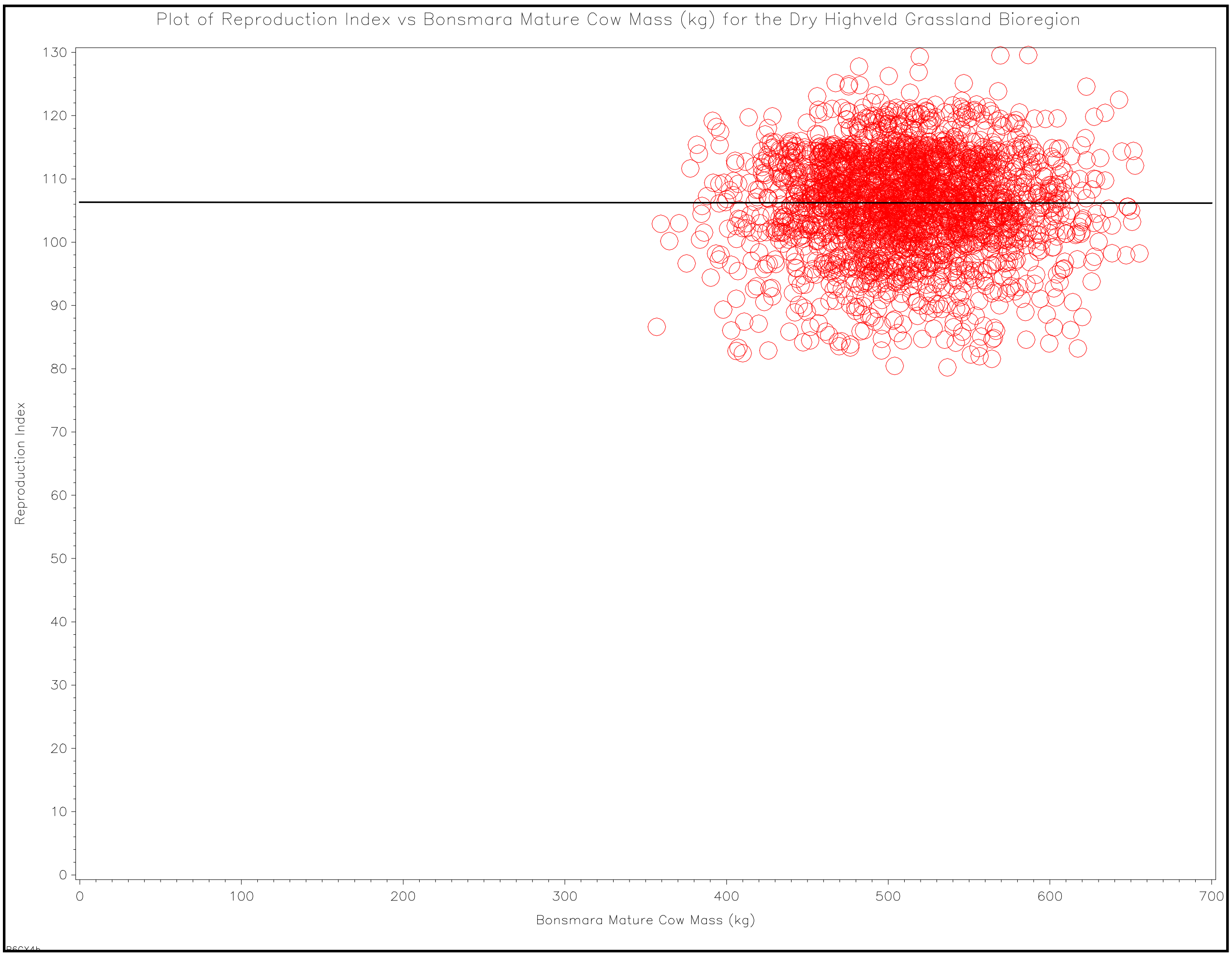

Figure 7.3 Linear relationship between Bonsmara cow MW_E and RI in the Dry Highveld Grassland

The results indicate that Bonsmara cow size has no influence on reproduction efficiency in the Dry Highland Grassland. The results indicate that mean Bonsmara MW_E in the Dry Highland Grassland is 512.3 kg which is higher than the Bonsmara mean of 499.5 kg. The RI mean of the Dry Highland Grassland is 106.2 is also higher than the total RI mean of 104.6. The results therefore seem to indicate that in the Dry Highland Grassland the mean Bonsmara MW_E of 512 kg is near to optimum for reproduction efficiency.

Cow size and reproduction in the Eastern Kalahari Bushveld

These results reveal that there is a positive linear relationship between MW_E and RI in the Eastern Kalahari Bushveld. The relationship is statistically significant ($p < 0.0001$) and is described as RI = 0.013(MW_E) + 100.41. The proportion of variation in RI explained by MW_E is, however, very small ($R^2 = 0.0066$). Linear regression output is shown in Figure 7.4.

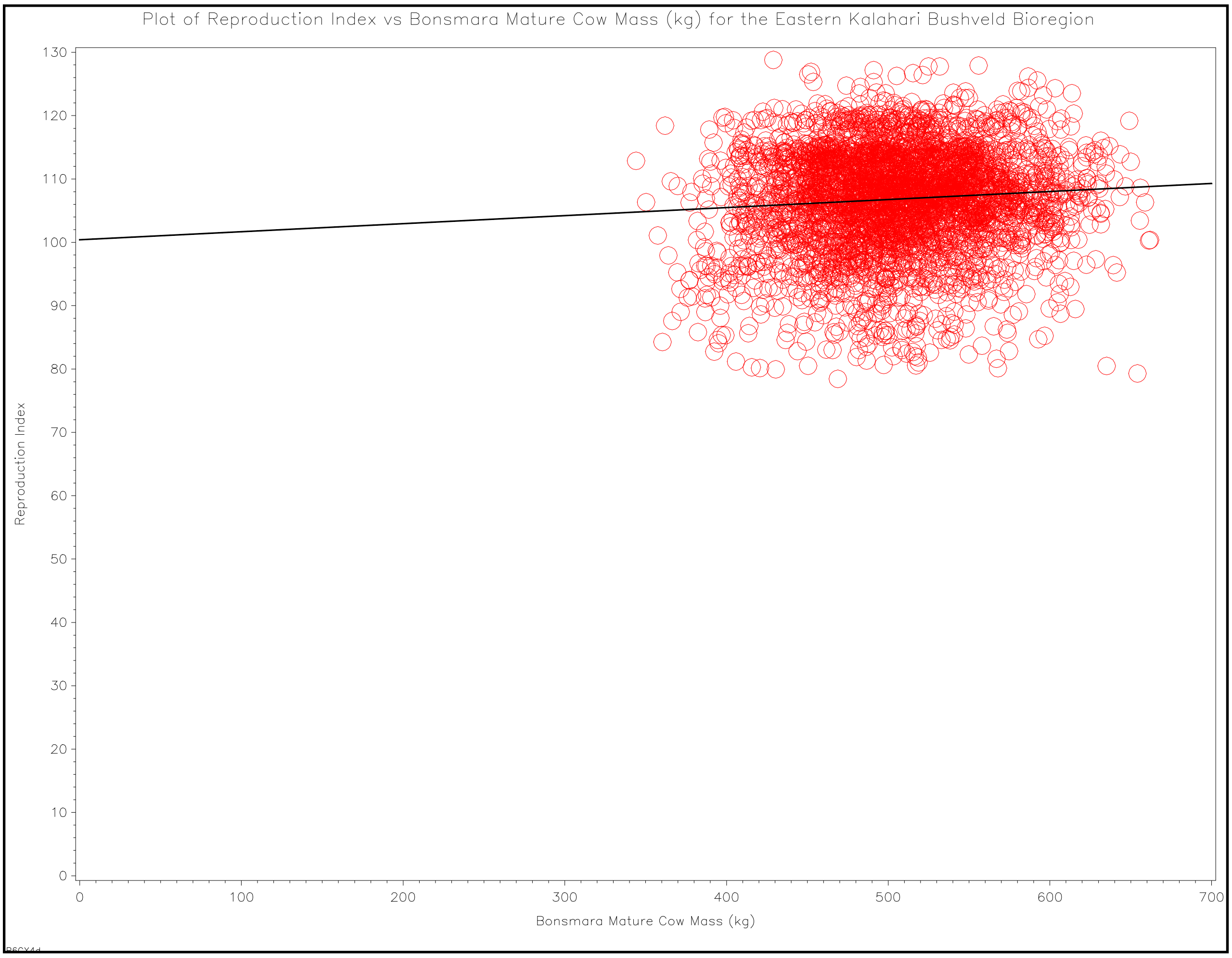

Figure 7.4 Linear relationship between Bonsmara cow MW_E and RI in the Eastern Kalahari Bushveld

The slight positive relationship indicates that there is a tendency for larger Bonsmara cows to be slightly more reproductive than smaller cows in the Eastern Kalahari Bushveld. These results indicate that mean Bonsmara MW_E in the Eastern Kalahari Bushveld is 506.3 kg, which is higher than the Bonsmara mean of 499.5 kg. The RI mean of the Dry Highland Grassland is 106.8, which is also higher than the total RI mean of 104.6. The relationship between cow size and reproduction is, however, slight. The results therefore seem to indicate that in the Eastern Kalahari Bushveld the mean Bonsmara MW_E of 506.3 kg is nearing optimum for reproduction efficiency.

Cow size and reproduction in the Mesic Highveld Grassland

These results reveal that there is a positive relationship between Bonsmara cow MW_E and RI in the Mesic Highveld Grassland. The relationship is statistically significant ($p < 0.0001$) and is described as RI = 0.031(MW_E) + 87.21. The proportion of variation in RI explained by MW_E is, however, small ($R^2 = 0.035$). Linear regression output is shown in Figure 7.5.

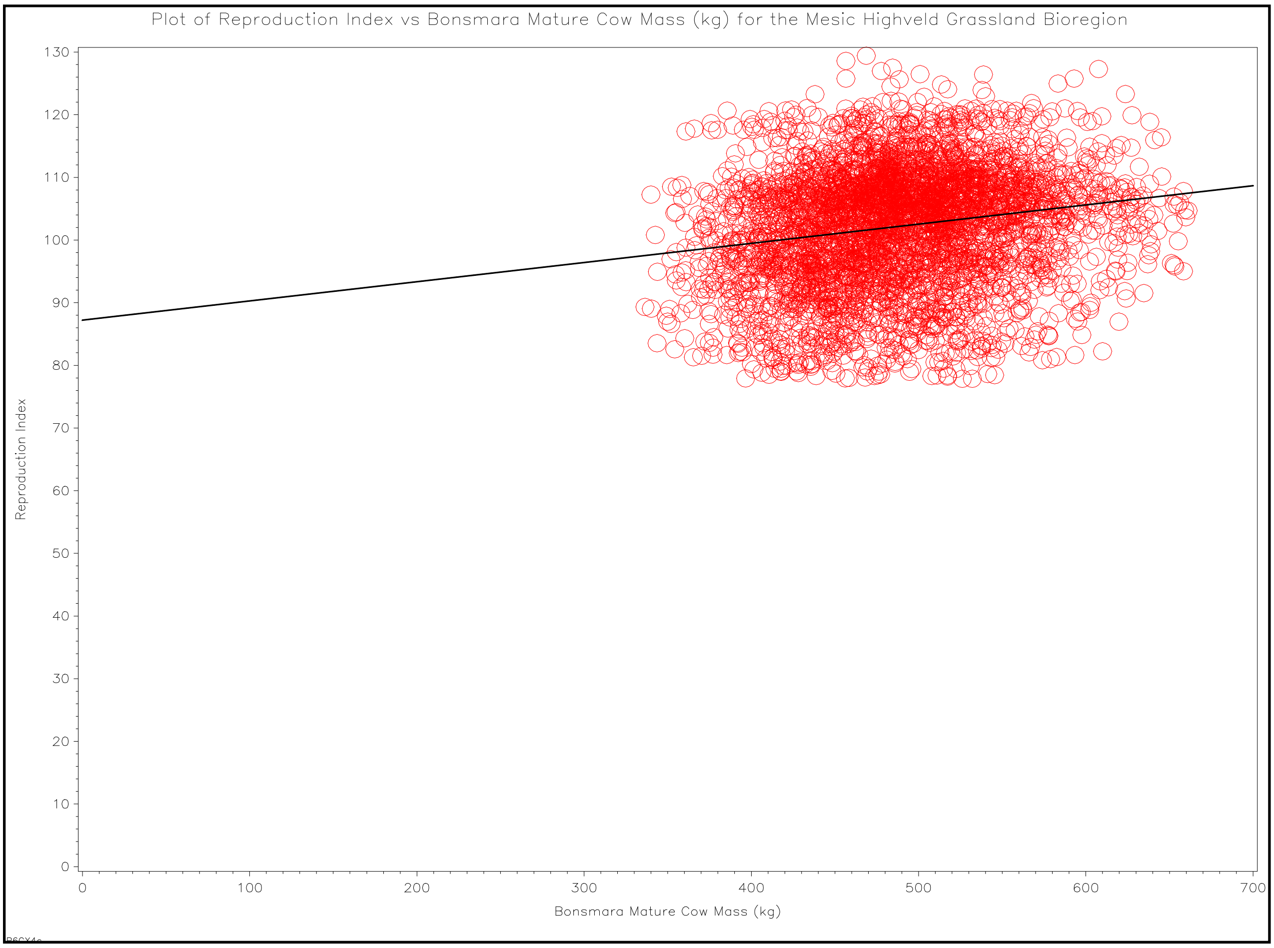

Figure 7.5 Linear relationships between MW_E and RI in the Mesic Highveld Grassland

The positive relationship indicates that larger Bonsmara cows are more reproductive than smaller cows in the Mesic Highveld Grassland. These results indicate that Mesic Highveld Grassland mean Bonsmara MW_E is 488.1 kg which is lower than the Bonsmara mean of 499.5 kg. The RI mean of the Mesic Highveld Grassland is 102, which is also less than the breed RI mean of 104.6. Selection for larger than current average sized Bonsmara cows in the Mesic Highveld Grassland should, therefore, lead to improved reproduction efficiency in the Mesic Highveld Grassland.

7.3. CONCLUSION: EFFECT OF MATURE SIZE ON THE REPRODUCTION EFFICIENCY OF BONSMARA COWS

The objective of this study was to determine whether mature cow size has an influence on the reproductive efficiency of Bonsmara cows in South Africa. The results of this analysis indicate that there is an overall positive relationship between the mature weight of Bonsmara cows and their reproduction efficiency.

The positive relationship between Bonsmara cow size and reproductive efficiency should be considered in light of the implications of the resource allocation theory proposed by Beilharz *et al.* (1993) and Fisher's (1930) fundamental theorem of natural selection. Beilharz *et al.*'s (1993) theory suggests that the environmental resources available for a population of animals, which was selected in a specific environment, are optimally distributed between the production and reproduction ability of the population. The environmental resources therefore determine the phenotype that can be sustained most efficiently. If the implications of the resource allocation theory is considered with those of Fisher's (1930) fundamental theorem of natural selection, the relationship between the environment, mature cow size and reproductive efficiency are put into perspective. Fisher's (1930) theory suggests that in a natural population, the reproductive fitness and body weight will be near the peak of fitness. Fisher's theory implies that when the population’s mean body weight is moved in either direction due to selection, the reproductive fitness of the population will decline (Falconer & King, 1953). The theories suggest that when the population mean cow size is increased past a limit set by the available environmental resources it will result in a decline in the mean of the population’s reproductive efficiency. The environmental resources available in a production region should consequently have a limiting influence on both the production and reproductive potential for a production region.

The environment’s limiting influence on the production potential of a production environment is well understood by most Bonsmara breeders. It is believed by most breeders that their cows should be of optimal size and adapted to their environment for them to express their full genetic potential (Bonsma, 1983). Taylor (2006) found that smaller- and medium framed Santa Gertrudis cows are reproductively more efficient than larger cows in extensive Southern African conditions (Tailor, 2006). The results of this study, however, suggest the opposite. The positive relationship found between the mature weight of Bonsmara cows and their reproductive efficiency indicates that there is a tendency for Bonsmara cows that are larger than average (499.5 kg) to be reproductively more efficient than smaller cows. This result is in accordance with the suggested optimal mature cow weight of Macgregor & Swanepoel of 500 – 510 kg.

The results of this analysis imply that the availible environmental resources do not have a restraining influence on the reproductive efficiency of Bonsmara cows in South Africa. This implication is unexpected and warrants futher discussion. It was shown that the South African beef production environment is considered nutritionally deficient (De Waal, 1990) due to low rainfall (Schulz, 1997) and prevailing soil properties (McDowel, 1996). The nutrients that are available to the cow are partioned in the following order: maintenance, growth, lactation, and then reproduction (Johnson *et al*., 2010). More than 50% of the total energy intake of adult cattle is required for body maintenance (Arango & Van Vleck, 2002). The higher maintenance requirement and nutrient partioning effect are therefore the reason why it is accepted that larger- framed cattle will have lower reproduction in environmentlly challeging environments (Jenkins & Ferrell, 1994; Taylor, 2006). Kleiber’s theory (1932), however, states that metabolic weight = live weight ^ 0.75. This indicates that although larger cattle have higher nutrient requirements, they are more efficient utilisers of nutrients. Under the conditions of this study it is therfore postulated that although the larger Bonsmara cows have higher maintenance requirements, the disadvantage of higher nutrient requirements is less than the advantage posed by the advantage of larger body reserves that can be utilised for reproductive processes.

CHAPTER 8

8.1. GENERAL CONCLUSIONS

This study used a number of novel techniques to investigate the influence of the South African production environment on the production efficiency of Bonsmara cows. The results confirmed the existence of a complicated relationship between the cow's physical environment and her production efficiency. Numerous interactions were found but only those interactions that could be explained were discussed in depth. It must be stressed that the conclusions of this study are only valid under the conditions in which the data were recorded. Those conditions represent well-managed Bonsmara stud cows that are extensively managed in the Central Bushveld-, Mesic Highveld-, Dry Highland Grassland- and Eastern Kalahari Bushveld bioregions of South Africa.

The influence of the environment on beef cow efficiency was highlighted in this study. It is perceived by many animal scientists and cattle breeders that the efficiency of a beef cow will be optimal when the cow's mature size is optimal for her production environment. The environment is therefore accepted to have a major influence on efficiency of beef cows. The results of this study, however, found the contrary. The study found that the influence of the individual breeders on production efficiency is far greater than the influence of production environment. Results indicate that the production region explains only 1% – 8% of the variation in the production traits investigated while breeder explained 12% – 30% of the variation in the same traits.

The study did confirm some of the well known environmental effects on extensive beef production. High rainfall (1% – 8%) and temperatures (1%) were shown to have a negative influence on the production efficiency of Bonsmara cows. The actual influence of temperature on production efficiency was, however, small but significant. The small influence of temperature is possibly an indication that Bonsmara cows are well adapted and that they do not suffer significantly from heat stress within the study area. The study population however only included reproductive, and per implication, adapted animals. The influence of temperature on production efficiency could therefore be higher than indicated in the study.

The quantifiable effect of the combined environmental characteristics on the production traits was shown to change (4% – 10%) with increasing age. It was argued that the larger the influence of the combined environment on a production trait, the larger the possibility to manipulate the expression of the trait through management practices. It was shown that wean- (9%) and yearling (10%) weights as well as AFC (7%) were the production traits that were influenced the most by the environment.

Rainfall was the environmental characteristic that numerically had the largest influence (8% – 9%) on those traits. The source of the negative influence of rainfall on the growth and reproduction traits is postulated to be due to the influence of high rainfall on the quality of winter grazing. The study also found that there is, contrary to popular belief, a slight positive relationship (0.025) between Bonsmara cow size and reproductive ability. This relationship indicates that there is a tendency for larger Bonsmara cows to be reproductively more efficient than smaller Bonsmara cows. It was postulated that this is an indication that the environment does not have a limiting influence on the reproduction efficiency of Bonsmara cows.

The overall conclusion of this investigation is that the production efficiency of a Bonsmara cow or herd is due to the management practices and breeding objectives of the breeder, rather than production environment. It was shown that the nutritional supplementation of heifers from pre-wean to post yearling age in higher rainfall areas has the greatest potential to improve the efficiency of Bonsmara herds. Selection for Bonsmara cows that is slightly larger than the current breed average should also lead to improvement in reproduction efficiency. With the correct management procedures and breeding objectives it is therefore possible to breed with highly efficient Bonsmara cows in any part of the main beef production regions of South Africa.

8.2. RECOMMENDATIONS

The study confirmed the influence of certain environmental characteristics on beef cow efficiency. The study indicates that high rainfall and temperatures have a negative influence on production efficiency. The mechanism behind the negative interaction between high rainfall and growth and reproduction traits could be investigated. The study highlights the small, negative influence that high environmental temperatures have on the growth and reproduction traits of Bonsmara cattle. This negative influence persists in spite of the high selection emphasis placed on adaptability by Bonsmara breeders since the inception of the breed. More research should therefore be focussed on developing protocols for more effective methods of identifying and selection for adaptive ability in beef cattle. The results also indicate that the management practices and breeding objectives of the breeders have a far greater influence on production efficiency of Bonsmara cows than the environment. An investigation into the management practices and breeding objectives employed by breeders to counteract the influence of the environment could be useful for improving the overall production efficiency of extensive managed beef breeds in South Africa.

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