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FACULTE UNIVERSITAIRE DES SCIENCES AGRONOMIQUES DE GEMBLOUX

Genotype by Environment Interaction for Production Traits of Holsteins Using Two Countries as Model: Luxembourg and Tunisia

Hedi HAMMAMI

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Résumé. La mondialisation entraîne une sélection et un échange de génotypes dans des environnements variés. Ignorer l'effet des interactions génotype x environnement (G x E) peut affecter les stratégies d'élevage et limiter l'efficacité de la coopération entre les programmes d'amélioration génétique. L'évaluation de l'efficacité de la sélection indirecte et des effets de G x E est donc nécessaire. L'objectif de cette thèse est d'évaluer l'importance de G x E pour le rendement laitier en utilisant la population Holstein du Grand Duché de Luxembourg et celle de Tunisie. En effet, ces deux pays basent leur programme d'élevage sur l'importation de matériel génétique d'origines variées. Cette étude requiert des données génotypiques et environnementales. L'étude des liens génétiques entre les deux populations a été réalisée dans la première partie de cette thèse. Les relations de parenté et la similitude génétique étaient importantes. Il est apparu que les liens génétiques s'étaient renforcés avec le temps ce qui a permis de réaliser l'analyse de l'expression phénotypique des filles de pères communs sous chacun des deux environnements étudiés. Dans une deuxième étape, les paramètres génétiques pour la quantité de lait, de matière grasse, et de matière protéique de la population Holstein tunisienne ont été estimés à l'aide d'un modèle de régressions aléatoires 'jour de test' (RRTD). Les valeurs d'héritabilité estimées à 305 jours pour le lait et ses composants étaient faibles à modérées (0,12 à 0,18). Ces valeurs reflétaient les difficultés rencontrées par les vaches hautes productrices pour exprimer leur potentiel génétique dans des conditions tunisiennes plus difficiles. Dans une troisième étape, l'interaction G x E pour le lait et la persistance a été étudiée en utilisant des modèles RRTD bivariés où le rendement laitier dans chaque pays était considéré comme un caractère différent. Un modèle père et ensuite un modèle animal ont été employés. Des effets G x E importants ont été détectés pour le rendement laitier et la persistance en utilisant ces deux modèles. Des différences significatives pour les variances génétiques et de l'environnement permanent entre les deux pays ont été observées. Les corrélations génétiques pour le rendement de lait à 305 jours et la persistance entre le Luxembourg et la Tunisie étaient de 0,50 et 0,43 (modèle père) et de 0,60 et 0,36 (modèle animal). Des corrélations de rang basses entre les valeurs d'élevage des pères communs ont été observées et traduisaient un classement différent des pères entre les deux pays. A la fin de cette thèse, un paramètre décrivant le management des troupeaux (reflétant lui-même le niveau d'intensité alimentaire et la technicité dans la gestion des troupeaux) a été utilisé. Trois environnements spécifiques à l'intérieur de chaque pays étudié ont été identifiés selon leur niveau de conduite. L'interaction G x E intra et inter-environnements a été étudiée. Des effets G x E ont été observés entre les trois niveaux tunisiens. Par contre, au Luxembourg, seule une hétérogénéité des variances génétiques associée à un reclassement limité des pères à travers les trois niveaux a été observée. En conclusion, cette thèse montre, que dans les systèmes de production à bas niveaux d'intrants et sous des effets environnementaux contraignants, la sélection des génotypes basée sur des caractères d'adaptation aux conditions spécifiques doit être préconisée**.** Si les conditions d'alimentation, de gestion et de conduite d'élevage sont favorables, un haut niveau de sensibilité environnementale est souhaité et l'élevage de races hautes productrices peut être encouragé.

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Summary. Under globalization, breeding organizations are selecting animals and exchanging germplasm across various environments. Ignoring genotype by environment interaction (G x E) may affect the efficiency of breeding strategies and limit outcomes from cooperation between breeding programs. Quantifying the effectiveness of indirect selection and effects of G x E for different breeds is therefore necessary. The objective of this thesis was to evaluate the magnitude of G x E for milk yield using Luxembourg and Tunisian Holstein populations. In fact, these two countries rely considerably on importation of superior genes from diverse origins for their breeding programs. This study needed records on both the genotype and the environment. In the first part of this thesis, genetic ties between the two populations were studied. Additive relationships and genetic similarity were important and genetic links have been strengthened with time which allowed the analysis of the phenotypic expression of daughters of common sires under each of these tow production environments. In the second part, genetic parameters for production traits of Tunisian Holsteins were estimated by a test-day random regression model (RRTD). Heritability estimates for 305-d milk, fat and protein yields were low to moderate (0.12 to 0.18) suspecting difficulties of high-producing cows to express their potential under limiting production conditions. In the third part, G x E for milk yield and persistency were investigated using character state models, where milk yield in each country was considered as a separate trait, and where the country border delimitation was designed as an environmental character state. A RRTD sire model was applied and was extended to a RRTD animal model. Significant G x E was detected for milk yield and persistency by both models. Large differences in genetic and permanent environmental variances between the two countries were observed. Genetic correlations for 305-d milk yield and persistency between Luxembourg and Tunisian Holsteins were 0.50 and 0.43 (sire model) and 0.60 and 0.36 (animal model). Moreover, low rank correlations obtained between estimated breeding values of common sires translate a significant re-ranking between the two environments. At the end of this thesis, a herd management (HM) parameter reflecting feeding and management intensity was defined. Three HM levels were identified in each country and G x E was investigated within- and across-environments. Significant G x E was detected between the Tunisian HM levels, whereas, only heterogeneous genetic variance for milk yield with limited re-ranking of sires across the three Luxembourg environments was observed. Overall, this thesis shows that under constraining environmental effects, selection for adaptive traits among economically valuable traits under their specific conditions is needed for low-input systems. When satisfactory feeding resources, management and husbandry practices are available, high degree environmental sensitivity is desired and the use of a high yielding breed may be encouraged.

I dedicate this work to my father and mother and I hope that they are satisfied and honored. This work is, therefore, partly a product of my father's labor and my mother's persistence and their great love to their child's. I owe this work to them.

I also dedicate this work to my wife Wahida and my little pearl Asma for enduring more than three years, and also for their patience, love, encouragement, and help. I cannot imagine that I could complete this work without love and support of my best friend and loving wife, Wahida Marzougui. I dedicate this work to you my love.

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List of Abreviations

AG = additive genetic
BV = breeding values
DIM = days in milk
F_e = effective number of founders
F_a = effective number of ancestors
EBV = estimated breeding values
G x E = genotype by environment interaction
GUE = Guernsey
HM = herd management
HOL = Holstein-Friesian breed
HY = herd-year common environmental
ICAR = International Commity of Animal Recording
ID = Reference identification
INTERBUL = International Bull genetic evaluation
MACE = Multi-trait Across-Country Evaluation
PE = permanent environmental
R = residual variances
RR = random regressions
r_g = genetic correlation
r_s = rank correlation
SPE = specific environment
SD = standard deviation
TD = test day
TDRR = test day random regression model

Chapter 1

General Introduction

H. Hammami

Animal Science Unit, Gembloux Agricultural University
Passage des Déportés, 2 B-5030 Gembloux, Belgium

In the future, purchasing power, urbanization, and consumer preference should be the most influential factor among the various drivers of change in animal production. At the 2030 horizon, developing countries may account for 85% of the human population. Milk production improvement rates from 2001 to 2030 are expected to reach 1.4% per annum worldwide and 2.5% in the developing countries (FAO, 2007). Economic globalization and government subsides will involve more exchange among the world markets in livestock, in production systems and management techniques, and livestock products.

Nowadays, there is a tremendous exchange of animal germplasm among developed countries as well as among countries in the North and South hemispheres. Gene flow driven by advances in reproductive technology should be also accelerated in the future. Exotic germplasm and high yielding breeds are used worldwide, often in replacement of local breeds to improve milk production.

According to the high variation in farming systems and management resources of dairy populations in the different regions of the globe, environmental effects have the potential to interact strongly with genotypes to alter production parameters. Efficiency and sustainability of breeding programs under this flow of exchange inter and intra environments are conditioned by the ability of genotypes to adjust sufficiently their phenotypes in response to changes in their new bio-physical conditions, and also by the capabilities of breeder's organization to manage genetic resources. Thus, breeders and farmers are urged to balance equitably between productive and adaptive characteristics of genetic resources. Therefore, genotype by environment interactions (G × E) should be taken into account and evaluated in different space and time horizons.

Furthermore, as the international trade with frozen semen increases, accurate and improved tools to compare animals across countries where G × E is accounted for become necessary. Presently, the Interbull Centre has considered the existence of G × E in routine evaluations of dairy cattle populations based on country member delimitation as a criterion for segregating different environmental character states (Interbull, 2007). However, given the diversification of production systems within countries and probable resemblance of some of these systems among countries, a different approach for defining a production environment ought to be used in order to account properly for G × E under various production circumstances. Nowadays only 26 out of the 42 Interbull country members participate in international genetic evaluations. Countries that are not participating at the Interbull evaluations have difficulties to choose foreign sires that are suitable for their production systems. König *et al.* (2005) gave a comprehensive review on within- and across-country G × E investigations. Unfortunately, nearly all studies on G × E using field data were carried out in developed countries of the Northern hemisphere. In spite of the large number of animals or semen exchange between Northern exporting and Southern importing countries, very little knowledge and feed-back about genetic "response" in the importing environments has been accumulated. A great deal of research work is required to investigate G × E that may occur between Northern and Southern production levels and systems, and also to quantify the effectiveness of genetic responses from indirect selection in different environments. Two model countries were used in this thesis for that purpose, Luxembourg as a Northern developed country and Tunisia as a Southern developing country. Both countries have comparable medium sized populations and are known by continuously importing foreign genes from various origins.

Luxembourg is one of the smallest countries in the European Union (EU). The dairy cattle industry plays a considerable role in Luxembourg agriculture economy. Holstein cattle, that were upgraded from Friesian and Red-white cattle, is the predominant dairy breed and more than 90% of the total dairy cattle are under a milk recording system. Breeding programs are based on importation of semen from different origins with few young bulls that are being locally tested over the last years. Genetic evaluation is done conjointly with the German dairy population. However, similarly to most EU countries, Luxembourg dairy sector is facing a period of significant changes due to three major decisions: the EU enlargement, the Common Agricultural Policy reform, and on-going World Trade Organization negotiations. Because of decoupling and intervention price cuts, the diversification of actual production systems is necessary. Some farmers will have to reduce production intensity while others will continue to be more intensive. The transition from one system to another should take into account adaptability and reaction of genotypes to various environments based on local studies when possible or by learning from experiences in other regions around the world.

Tunisia had opted, to enhance dairy milk production, by importing since the 1960's cows at the beginning essentially Friesians later switching to Holsteins, and thereafter has continuously imported pregnant Holstein heifers and semen from various origins (European and North American countries). The dairy industry has been developing, milk factories were created and many cooperatives were implemented to manage production, collection and marketing of milk. Fresh and regenerated milk imports were called off in 2001 because milk production reached self-sufficiency levels. Unfortunately after a few years, sporadic importation of fresh milk and pregnant heifers had to be restarted. Even though the dairy sector has shown some satisfactory performances, it remains sensible to limited feed resources and integrated livestock-farming. Moreover, the lack of a stable genetic improvement policy remains the main weakness for the improvement of genetic resources in the country. Selection and replacements are based on phenotypic performances and depend on herd owner decisions. The importation of pregnant heifers (3,000 heads per year) remains the solicited solution to meet instantaneously emerging demands. Semen is being imported from temperate regions in important quantities (250,000 straws per year) and semen selection is based on Interbull conversion formulas developed for EBV from the USA (OEP, 2007). Nevertheless, selection strategies should logically operate according to local production circumstances taking into account worldwide market tendency and environmental sensitivity of imported genes to local environment in order to generate sustainable breeding programs.

Aim of this thesis

The overall objective of this study was to investigate genotype by environment interaction for milk production traits in two model countries, Luxembourg and Tunisia, in order to test the usefulness of differential selection.

Outline of this thesis

This thesis is presented as a compilation of original articles published or submitted for publication in national and international peer-reviewed journals. The thesis starts with a review of the literature in Chapter 2. This review focuses on definition and theory, methods applied and scope of G × E in dairy cattle as reported in major works using field data. The implication of G × E for dairy cattle breeding programs is also discussed.

Most studies were realized within or between Northern hemisphere countries where genetic links exists due to undergone selection across these countries. Therefore technically sound studies using large data modelling were possible thanks to data availability at the Interbull Centre. However investigations on G × E between northern and southern countries were rare and nearly no studies focused on the importance of G × E in importing countries.

High genetic links among Holstein populations in developed countries, resulting from direct or indirect cooperation in breeding programs, are well known. However, information on genetic links and variability among Holstein populations in countries with emerging dairy industries or between populations of importing and exporting countries are scarce. The first step of this study presented in Chapter 3 was to **investigate the genetic diversity and links between Luxembourg and Tunisian Holsteins** known both as importing countries of germplasm from various origins however different as Luxembourg is a typical Northern country and Tunisia is an emerging Southern country.

Quantifying G × E needs performance measures on similar genotypes producing under at least 2 distinct environments. Thus, modelling performance data available (test-day records) from Luxembourg and Tunisia is necessary for genetic evaluation. Luxembourg runs joint genetic evaluation with Germany with a model that provides sires EBV for Interbull runs. On the other hand, Tunisia lacks currently a model for genetic evaluation even though it has a milk recording and data processing centre operating for many years. Thus, the second part of this thesis begins in Chapter 4 and focuses on **the estimation of genetic parameters of Tunisian Holsteins** based on a multi-trait-multi-lactation random regression test-day model.

Such a model was thereafter used for a first investigation of G × E using Luxembourg and Tunisian populations considering a whole country as character state different from the other one. Most links between the 2 populations studied here were building up because of the use of semen from common sires proven in different exporting countries. Therefore, the objective of the article presented in Chapter 5 was to **assess G × E by within- and across-country test day sire models**. In Chapter 6, the sire model was extended to an animal model and **G×E was assessed for first lactation milk yield using Luxembourg and Tunisian field data in a test-day random regression animal model**. In Chapter 7, a herd management parameter was defined to evaluate G × E across- country production systems. Therefore, the objective of the latter paper was to **evaluate the environmental sensitivity for milk yield in Holsteins using herd management levels within and between contrasted environments in Luxembourg and Tunisia**.

The thesis ends with a general discussion in Chapter 8. The main focus is on results obtained on G × E and their implications for breeding programs, especially in Luxembourg and Tunisia as a model.

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Chapter 2

Genotype by Environment Interaction in Dairy Cattle

FROM:

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2.1. Abstract

2.1.1. Genotype by environment interaction in dairy cattle

The aim of this literature review was to identify the existence and scope of genotype by environment interaction (**G × E**) from reports on dairy cattle populations in different management systems. Methods applied to deal with G × E (controlled experiments and large data modelling) were discussed. A G × E was confirmed essentially when high differences between production environments and/or genotypes (genetically distant genotypes) were observed. Environmental effects were aggregated in most studies and identification of the components of the environment was largely unresolved, with only a few studies based on more definite-descriptors of environment. The implications of G × E on breeding decisions are discussed. Breeders should select genotypes on production traits within environmental conditions comparable to where candidate animals are intended to perform.

Keywords: genotype by environment interaction, genetic correlation, reaction norm, dairy cattle, breed, selection.

2.1.2. Interactions entre Génotype et Environnement chez les Bovins Laitiers

Cette revue bibliographique a permis d'identifier la présence de G × E chez les bovins laitiers à partir des performances phénotypiques enregistrées dans différents environnements. Les méthodes utilisées pour l'investigation de G × E ont été discutées. L'importance et l'échelle de grandeur de ces interactions basées sur l'utilisation de ces méthodes sont signalées. L'existence de G × E est essentiellement confirmée en présence de grandes différences entre les environnements de production et/ou de distances génétiques entre les génotypes. Les effets environnementaux ont été agrégés dans les différentes études avec une identification assez synthétique des composants du milieu excepté quelques travaux récents utilisant une définition plus fine de l'environnement. Les implications de G × E sur les programmes de sélection sont discutées. Les éleveurs devraient sélectionner les génotypes dans les conditions environnementales dans lesquelles ces candidats reproducteurs seront élevés en utilisant un index de sélection combinant les caractères de production et les principaux autres caractères économiques.

Mots clés : interactions génotype x environnement, corrélation génétique, norme de réaction, bovin laitier, race, sélection.

2.2. Introduction

Milk production will need to nearly double in the world over the next decade to follow population and income growth. The strongest demand for milk and milk products are anticipated for developing countries where an important population growth is expected (Tollens *et al.*, 2004). In addition, internationalization and world globalization will lead to an even freer world dairy market and an enlargement of germplasm exchange in the world. This situation would be translated by an increased intensification and industrialization of production systems and will consequently have profound implications on production systems and the environment. However, the sustainable intensification requires appropriate use of genetic resources with an understanding of the limitations and opportunities of the production environment in which the animals will be maintained. The ability of farmers to respond to environmental conditions such as climate, feed base, food security, and consumer preferences should guarantee a sustainable livestock development.

In recent decades, dairy cattle breeding have become an increasingly international business and a substantial exchange of Holstein semen has taken place worldwide (Powell and Sieber, 1994). On the other hand, performances of daughters of AI bulls are recorded in various environments in the world. Selection of superior animals, chosen on breeding values from national evaluations, has been operating within countries. However, Banos and Smith (1991) reported that across country selection is more profitable under the globalization of dairy industries. Currently, the multiple-trait across country evaluation (MACE) procedure (Schaeffer, 1994) is used by Interbull. This routine evaluation incorporates information on daughters of bulls from different Interbull country members. Then, genetic correlations between countries are estimated from common bulls and three-quarter sibs that have progeny in multiple countries. The international bull breeding values can then be converted to national scales. Thus, using the international evaluation, foreign bulls can be reliably selected for national use. Lohuis and Dekkers (1998) estimated that the global selection can increase rates of genetic response by up to 17% compared to within-country selection.

In the absence of genotype by environment interaction (**G × E)**, the expected genetic correlation across environments is one. Cooper and Delacy (1994) reported that only when the genetic correlation among environments is less than one does the G × E impede response to selection. With the current international genetic evaluation of bulls (Interbull), the national trait measures are viewed as different traits depending on the location of herds and using the country member borders as the criterion for differing among environments. Such procedures are ignoring the differences between herds in the same country especially in large countries. It also ignores the similarities between many herds within and between countries (Weigel and Rekaya, 2000; Fikse *et al.*, 2003; Zwald *et al.*, 2003a).

Tropical and developing countries often rely on exotic germplasm for breeding purposes. They however have climatic conditions, production systems, and markets different from those where animals were evaluated. Thus, the G × E can cause a reduced efficiency of their genetic improvement programs. The investigation of G × E in order to thwart this fact was limited and concerned mainly large populations in the northern hemisphere and in a few tropical countries.

The objective of this paper was to review methods used to study G × E, to asses the importance of G × E, and to determine its effect on the efficiency on selection programs.

2.3. Genotype by environment interaction: Definition & theory

G × E occurs when performances of different genotypes are not equally affected by different environments (Falconer, 1952). The ability of living organisms (plants or animals) to alter the phenotype in response to changes in the environment is known as phenotypic plasticity or environmental sensitivity (Falconer and Mackay, 1996). When the same genotypes develop different phenotypes in different environments, then there is G × E. When the differences between genotypes vary between environments without changes in their ranking there is scaling effect (Figure 1). However, if the genotypes rank differently in different environment, the effect of G × E is re-ranking of individuals (Figure 2). G × E is of less importance if only scaling effect is obtained because the best selected individuals in one environment would still perform the best in other environments.

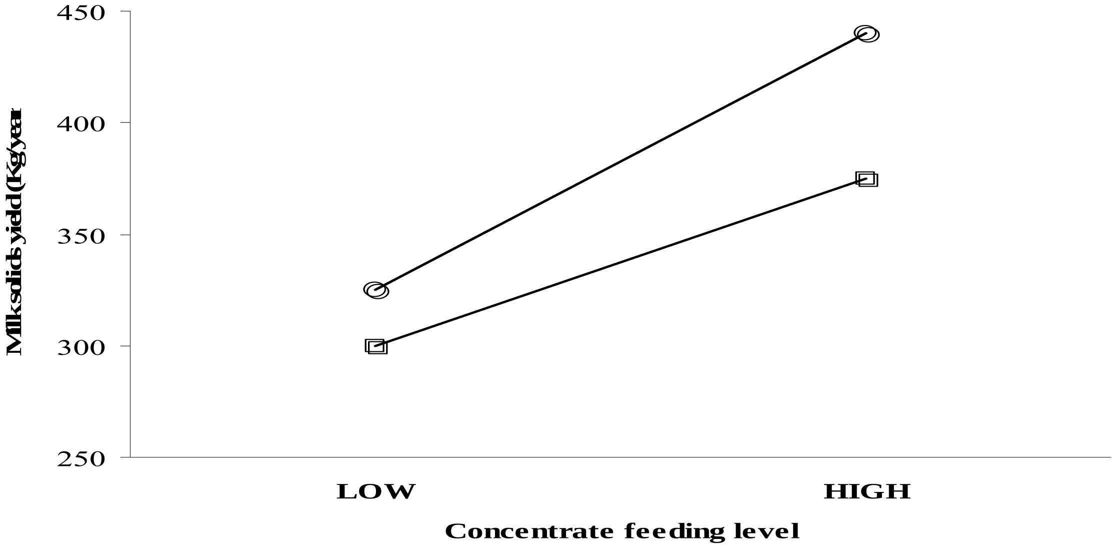

Figure 1. *Scaling effect for milk solids yield in high genetic merit (Circles) and low genetic merit (Squares) dairy cattle in systems with a low or high concentrate feeding level (Fulkerson et al., 2000).*

Figure 1. *Effet d'échelle pour la quantité de lait chez des bovins laitiers avec haut potentiel génétique (Cercles) et bas potentiel génétique (Carrés) dans un système d'alimentation à haut ou bas niveau de concentré (Fulkerson et al., 2000).*

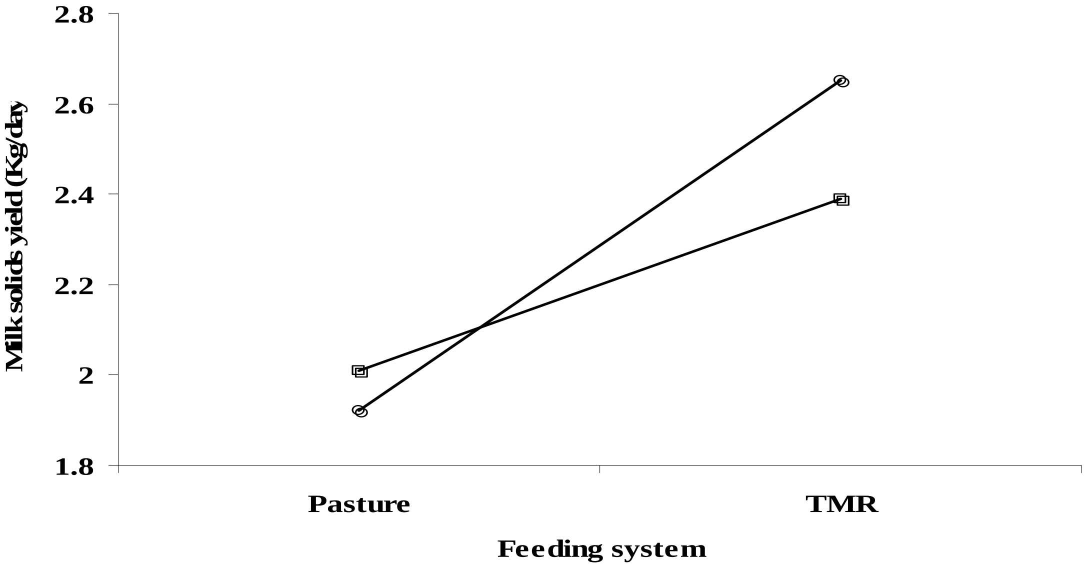

***Figure 2**. Re-ranking for milk solids yield in New Zealand Holstein Friesian (Circles) and North American Holstein Friesian (Squares) dairy cattle in a pasture-based or total mixed ration (TMR) system in early lactation (Kolver et al., 2002).*

***Figure 2**. Reclassement pour la quantité solide de lait observé chez les vaches primipares Holstein Néo-Zélandaise (Cercles) et Nord Américaine (Carrés) alimentées en pâturage ou au moyen d'une ration totale mélangée (TMR). (Kolver et al., 2002).*

The choice of environment or genotype characterisation depends on the aim of each study. Genotype can refer to a genotypic unit (breeds, crossbreds, individuals), but also to a genotypic value (individuals with certain phenotypic or genotypic performances, QTLs, genes). In the same way, environments could be defined as a unit (herd, region, country etc.), but also as a continuous value (temperature, rainfall, concentrate, feeding level, etc.). Lin and Togashi (2002) reported that genotype could be classified into three levels in combination with the environment. 1) Breed by environment interaction (between-breed interaction), 2) individual by environment interaction (within-breed interaction) and 3) gene by environment interaction (within-individual interaction). The usual elementary unit for definition of environment in dairy cattle is the herd. Using individual characteristics of each herd as a different environment will lead to great difficulties in comparing different environments.

Grouping herds according to their environmental similarities can be an alternative, but availability and accuracy of G × E determinism will depend on the "robustness" of the criterion used for their clustering. In the literature, these characteristics varied from a global, specific, to more detailed definition. Environments have been defined both as between countries with large climatic differences (Stanton *et al.*, 1991; Cienfuegos- Rivas *et al.*, 1999; Costa *et al.*, 2000; Rekaya *et al.*, 2001) as well as within country (Carabaño *et al.*, 1990; König *et al.*, 2005; Gernand *et al.*, 2007). Specific characteristics that have been examined include average herd level, herd size, feeding systems and levels, management, and housing systems (Hill *et al.*, 1983; Cromie *et al.*, 1998; Pryce *et al.*, 1999; Boettcher *et al.*, 2003; Fatehi *et al.*, 2003; Hayes *et al.*, 2003; Nauta *et al.*, 2006). A more limited herd environment characterization based on fine-definite environment descriptors applying canonical correspondence analysis, factor analysis, or principal component analysis, were recently introduced. This approach allow clustering of herds based on fine-definite farm characteristics and might be more efficient and realistic (Weigel and Rekaya, 2000; Zwald *et al.*, 2003b; Windig *et al.*, 2005; Haskell *et al.*, 2007).

The relationship between variations of the phenotypic expression of a genotype under continuous value of the environment is often shown as a reaction norm (Kolmodin *et al.*, 2002). In that case, the phenotypic expression of a genotype is viewed as a function of an environmental parameter (temperature, concentrate). If phenotypes change gradually or continuously over an environment gradient, the reaction approach is appropriate (de Jong, 1995). Plastic genotypes are known by highly variable phenotypes across environments, whereas robust or stable genotypes are known by relatively constant phenotypes across environments (de Jong and Bijma, 2002). When genotypes have significant differences between the quantitative measures of the phenotypic plasticity, then there is a G × E interaction. Differences in the phenotypic plasticity could be explained by the fact that some alleles may only be expressed in some specific environment. Favorable genes in some environments may become unfavorable under other environment conditions. Via *et al.* (1995) recognize that gene regulation may change depending on the environment.

2.4. Measures of genotype by environment interaction

To study G × E, records on both the genotype and the environment are required. The performance of a genotype (i.e. cow) cannot be recorded simultaneously in more than one environment (i.e. countries or regions). Because of the extensive use of AI in the dairy industries, daughters of the same sire are spread in different herds around the world.

Nevertheless, performances are obtained according to milk recording schemes based on “universal” guidelines. Information on the environment in which the record was taken is still less “detailed”. To overcome the lack of detailed information obtained from routine milk recording data, G × E measure can be based on experiments. A compromise between costs, availability of data, and experimental unit scale should be taken into account.

2.4.1. Controlled experiments

The most reported experimental studies investigating the existence of G × E in dairy cattle have taken place in experimental farms in Netherlands, Australia, Ireland, and New Zealand. The genotype was generally defined as a different strain of Holstein-Friesian and compromised specific groups based on the level of genetic merit. Environments were usually defined based on differences in feeding level and system. Experimental designs and protocols were involved hundreds of animals. Published results on the lack or existence of G × E concerned milk production (Veerkamp *et al.*, 1995; Kolver *et al.*, 2002; Beerda *et al.*, 2007), body score condition (Veerkamp *et al.*, 1994; Horan *et al.*, 2005; McCarthy *et al.*, 2007a), body dimensions, body weights and puberty (Macdonald *et al.*, 2007), health, fertility (Pryce *et al.*, 1999; Ouwesltjes *et al.*, 2007), and energy balance (Berry *et al.*, 2007; Beerda *et al.*, 2007). Most of these studies used differences in coefficients from regressing phenotypic performances on environments as indicators of G × E. In general, using experimental herds is expensive but more illustrative. On the other hand, results ought to be viewed as representing a genetic group “strain” and should be cautiously extrapolated out to the general population.

2.4.2. Modeling genetic variation

There are three main methods used for estimating G × E: interaction model, character state model, and reaction norm model. These models can be viewed as an extension of the simple and traditional genetic model for quantitative traits in which the phenotype (P) is considered as the sum of only independent genetic (G) and environmental effects (E) [P = G + E] (Falconer and Mackay, 1996).

The interaction model represents an extension of the traditional genetic model by an inclusion of the random interaction of genotype and environment and thus P = G + E + G × E. The most famous application is the use of the sire x herd interaction (Van der Werf and Ten Napel, 1991; Dimov *et al.*, 1995). With unbalanced data and in the presence of heterogeneity of variances among environments (herds), the interaction interpretation is difficult when applying this model (Dickerson, 1962). The sire x herd method permits a global description of the effect without allowing individual variations. In addition, the genetic additive relationships among sires are not considered in the estimation of G × E which is only an additional environmental effect.

Genes may show different expressions under different environments. Falconer (1952) described the expression of a trait in different environments as different characters, or ‘character states’. Thus, the performance of animals in different environments should be regarded as separate traits. Therefore, with the character state model, the genetic correlation between the same types of performance but measured in different environments is used to measure the G × E. The animal breeding analogy with the character state model is the multi-trait model, where performances in different environments are regarded as different and genetically correlated traits. With the character state model, the total additive genetic variance of the plastic trait among environments can be partitioned into the genetic variances of the character states within each environment and the genetic covariance between environments. The later is related to the G × E variance (de Jong and Bijma, 2002). When only two environments are studied, a bivariate analysis is the method for estimating genetic correlation. If more than two environments are involved, a multivariate analysis is applied and genetic correlation can be estimated for any pairs of environment combinations. A well known application of the character state model is the estimation of bulls' breeding values by Interbull using the Multiple Across Country Evaluation (MACE). Each country is considered as a different environment and the correlation between all pairs of country combinations is estimated. The character state model is known by the flexibility of its variance-covariance structure. However, the number of environments should be kept limited to meet computation requirements and convergence limitations. Moreover, this model is restricted to discrete environments and requires their classification into groups. The accuracy of correlation estimates between environments depends on the best representation of these groups. Clustering methods can be used to group environments with reference to major environments descriptors (e.g. Weigel and Rekaya, 2000; Zwald *et al.*, 2003b; Haskell *et al.*, 2007).

The reaction norm model was recently introduced to study G × E in animal breeding. This model expresses the phenotype as a polynomial function of the environmental value, where the polynomial coefficients are assumed to be under genetic influence (de Jong, 1995). The reaction norm model is efficient when phenotypes vary continually or gradually over an environmental gradient. It has an analogy with the random regression model, which could explain the recent introduction of the reaction norm model that originates from evolutionary biology in the beginning of the 19th century (Woltereck, 1909), in animal breeding (Strandberg *et al.*, 2000; Kolmodin *et al.*, 2002; Calus *et al.*, 2002). With reaction norm model, covariance functions (Kirkpatrick and Heckman, 1989) are used to model genetic effects over the environmental gradient changes. Breeding values for the coefficients of the function describing the reaction norm and the (co)variances of those coefficients are also estimated. The grouping of environments can be avoided when applying reaction norm model. In addition, the latter model can better explain differences among genotypes in response to external environment parameters (i.e. temperature, humidity). Studies of heat stress and genetic variation in heat tolerance (Ravagnolo *et al.*, 2000; Ravagnolo and Misztal, 2002; Bohmanova *et al.*, 2007) are relevant examples.

Mulder (2007) gave a comprehensive review of advantages and disadvantages of models dealing with G x E reported in the literature. The author presented six criteria for using a scoring scale for model comparison (Table 1). The best scored models were the multi-trait and the reaction normal model. de Jong (1995) stated that the reaction norm model is more appropriate for the study of graded responses in continuous environments, whereas the character state model (multi-trait model) is most appropriate to model discrete responses to discrete environments.

Table 1. *Comparison of models for G × E between macro-environments (Mulder, 2007)*

Tableau 1. *Comparaison des modèles d'estimation des interactions génotype x environnements entre les macro-environnements (Mulder, 2007)*

Criterion	Models		
	Interaction model	Multi-trait model	Reaction norm model
Nature of environmental scale	Class	Class	Continuous
Estimation of G × E	0/-	+	0
Flexibility variance-covariance structure	-	+	0
Predictability of phenotype	-	0	+
Biological interpretation of G × E	-	0/+	+
Genetic interpretation of G × E	-	+	0
Selection on macro-environmental sensivity	-	0/+	+

(+) best model, (-) worst model, and (0) model in between.

2.5. Genotype by environment interaction in dairy cattle

Experiments on dairy cattle reported in the literature dealt mainly with genotype by feeding level and system interactions. Two different diets varying in the dry matter proportion of concentrates, brewers' grains and silage were fed to a herd of two genetically distinct groups based on merit (Veerkamp *et al.*, 1994; Pryce *et al.*, 1999). In general, the G × E interaction exhibited was mostly a scaling effect and there was no significant interaction between diets and lines. In contrast, Veerkamp *et al.* (1994) reported significantly different regression coefficients of body score condition on pedigree index for fat and protein yield between the two diets. McCarthy *et al.* (2007a) studied the effect of three Holstein-Friesian strains (high production North American, high durability North American, and New Zealand Holstein-Friesian) and feeding system (high grass allowance feed system, increased stocking rate system, and increased concentrate supplementation) on body weight and body condition score. These authors found that the New Zealand strain remain the most suitable to low cost grass-based system, a predominant system in Ireland. Their study extended previous results found on a subset of the same data and confirmed significant effects of strain of Holstein-Friesian and feed system on reproduction performance (Horan *et al.*, 2004), milk production (Horan *et al.*, 2005), grass dry matter intake (Horan *et al.*, 2006), and somatic cell scores (McCarthy *et al.*, 2007b). All these studies reported important strain by environment interactions. Cows of New Zealand origin produced less milk than North American ones, but had better reproductive performances. Kolver *et al.* (2002) reported also a re-ranking of New Zealand and North-American genotypes between grazing and mixed ration. Macdonald *et al.* (2007) compared growth parameters between three different strains of Holstein-Friesian cows grazed on pasture in New Zealand. They concluded that differences in growth parameters and puberty exist among the different genetic strains studied when grazed on pasture.

In more comprehensive studies (large scale studies), the number of factors differing across environments is large compared to controlled experiments. This is the case in large countries with diverse climatic conditions and production systems. Within country analyses of G × E have been based on modelling data using essentially multi-trait models. Correlations between different environments were used to estimate G × E interactions. König *et al.* (2005) summarized correlations obtained on intra country analyses for milk traits in temperate countries. Stratification of herds varied by study and was based on: within herd-year mean for mature equivalent milk yield (Castillo-Juárez *et al.*, 2000; Ceron-Munoz *et al.*, 2004), within herd-year standard deviation for mature equivalent milk yield (Raffrenato *et al.*, 2003), regions (Carabaño *et al.*, 1990; Rekaya *et al.*, 2003; König *et al.*, 2005), production level (Calus *et al.*, 2002; Kolmodin *et al.*, 2002); herd size (Gernand *et al.*, 2007), test-day production levels (Veerkamp and Goddard, 1998; Hayes *et al.*, 2003), feeding regimes (Cromie *et al.*, 1998; Boettcher *et al.*, 2003; Fatehi *et al.*, 2003). Estimates of genetic correlations between environments as defined above were high (>0.80) showing little or no evidence for strong G × E. Almost all the within-country analyses reported only a scaling effect for milk yield with large heterogeneity of variances and in some case heterogeneity of heritability estimates was observed. For example, Boettcher *et al.* (2003) reported a scaling effect for milk yield with the largest genetic variance and heritability obtained in the conventional systems. The latter authors concluded a lack of presence of G × E between grazing and conventional management systems. In consequence, they reported that selection of sires on grazing systems can be accurate using the national breeding values applied for conventional systems.

Most of the between-country analyses estimated genetic parameters of traits for each environment studied. However, relationships between traits may also differ by environment. Thus, selection for high production in one environment may lead to different changes in correlated traits under different environments. To avoid this problem, the best way will be to model the relationship between several traits between different environments (Oseni *et al.*, 2004). Recently G × E has been observed for the association of milk yield with protein, fat yield and somatic cell score (Castillo-Juárez *et al.*, 2000; Raffrenato *et al.*, 2003), milk yield with fitness traits (Castillo-Juárez *et al.*, 2000; Windig *et al.*, 2005; Beerda *et al.*, 2007), milk yield with age at first calving (Ruiz-Sánchez *et al.*, 2007). Castillo-Juárez *et al.* (2000), reported changes in correlations between milk production and somatic cell score and conception rate with specific environments. These correlations were small between pairs of traits in favorable environments and were high in less favorable environments. These authors suggested that an improvement of the management in low environments can reduce the unfavorable correlation found between milk yield and somatic cell score and conception rate.

The use of germplasm selected in regions with differing climatic conditions and production systems (Bondoc *et al.*, 1989) may result in G × E that could reduce the efficieny of genetic improvement programs in the area where animals will produce. König *et al.* (2005) summarized genetic correlations for production traits estimated between countries reported in most studies investigating G × E (Table 2). Genetic correlations between the northern hemisphere group (Canada, USA, and Western Europe) ranged between 0.85 and 0.90 (Fikse *et al.*, 2003). Genetic correlations of less than 0.8 were found between North and South America (Stanton *et al.*, 1991; Cienfuegos-Rivas *et al.*, 1999; Costa *et al.*, 2000; Ceron-Munoz *et al.*, 2004) and between some eastern European countries (Rekaya *et al.*, 2001).

Low genetic correlations were obtained between countries that differ considerably in climate, management, and production system. Genetic correlation between Mexico and USA was 0.63 (Cienfuegos-Rivas *et al.*, 1999) and 0.49 between Kenya and the United Kingdom (Ojango and Pollot, 2002). Most of these studies pointed out the existence of a scaling effect of G × E, where response to selection was smaller in low input environments than in high input ones. Selection responses to the use of selected US Holstein sires for milk production in Latin America were estimated to range from 53% to 78% of the response observed in the USA (Stanton *et al.*, 1991). In Kenya, the response to selection based on UK breeding values was only 44% (Ojango and Pollot, 2002).

In a more comprehensive study on between-country analyses, Weigel *et al.* (2001) found high genetic correlations (>0.80) between milk yields across 17 Interbull country members. Estimates reported were higher than 0.90 between countries with predominantly grazing systems (i.e., Ireland, Australia, New Zealand). Correlations were also greater than 0.91 between countries with high milk production (US, Canada, Belgium, The Netherlands, and Italy). Correlations between remaining Interbull members ranged between 0.8 and 0.9.

Table 2. *Genetic correlations for production traits between countries (König et al., 2005)*

Tableau 2. *Corrélations génétiques entre différents pays pour la quantité de lait (König et al., 2005)*

References	Breed[1]	Milk trait	Country 1	Country 2	Genetic correlation
Carabaño *et al.*, 1989	HOL	305-d	Spain	US	0.82
Stanton *et al.*, 1991	HOL	305-d	US	Latin America[4]	0.82
			US	Latin America	0.91
			US	Latin America[5]	0.89
			US	Colombia	0.78
			US	Mexico	0.90
Charagu and Peterson, 1998	HOL[2]	BV, milk	Canada	New Zealand	0.29
	HOL[3]		Canada	New Zealand	0.25
Cienfuegos-Rivas *et al.*, 1999	HOL	305-d	US	Mexico[4]	0.60
			US	Mexico	0.63
			US	Mexico[5]	0.71
			US[5]	Mexico[4]	0.72
			US[5]	Mexico	0.69
			US[5]	Mexico[5]	0.93
Costa *et al.*, 2000	HOL	305-d	US	Brasil[4]	0.79
			US	Brasil	0.85
			US	Brasil[5]	0.87
			US[4]	Brasil[4]	0.72
			US[4]	Brasil[5]	0.86
			US[5]	Brasil[5]	0.88
Rekaya *et al.*, 2001	HOL	305-d	Estonia	Israel	0.74
			Austria	Israel	0.74
			Austria	Estonia	0.79
			Estonia	Finland	0.84
			Switzerland	Israel	0.83
			Czech Republic	Finland	0.82
			Switzerland	Estonia	0.83
			Czech Republic	Estonia	0.75
Ojango and Pollot, 2002	HOL	305-d	Kenya	United Kingdom	0.49
Fikse *et al.*, 2003	GUE	305-d	Australia	Canada	0.90
			Australia	US	0.87
			Australia	South Africa	0.87
			Canada	US	0.87
			Canada	South Africa	0.78
			US	South Africa	0.86
Ceron-Munoz *et al.*, 2004	HOL	305-d	Brazil4	Colombia[4]	0.72
			Brazil[5]	Colombia[5]	0.81
			Brazil[4]	Colombia[5]	0.77
			Brazil[5]	Colombia[4]	0.73

[1] *HOL=Holsteins; GUE=Guernsey* [2] *HOL=Canadian Holsteins* [3] *HOL=New Zealand Holsteins.*

[4] *Data set include herds with low herd year standard deviation.*

[5] *Data set include herds with high herd year standard deviation.*

2.6. Implications of genotype by environment interaction in dairy cattle

Regardless of the approach applied, the scaling effect of G × E was frequently reported. However, some studies did report the re-ranking effect (Carabaño *et al.*, 1989; Cienfuegos-Rivas *et al.*, 1999; Kolver *et al.*, 2002). In case of scaling effect, animals will maintain their ranking among environments but only differences in the magnitude of breeding values is observed. Pre-adjustment in the data (Wiggans and VanRaden, 1991) or correction in the evaluation model (Meuwissen *et al.*, 1996) is able to absorb the scaling effect, and thus the G × E is taken perfectly into account with no consequences on selection decisions. However, weights on traits within a composite index have to be defined with care when a scaling exists for some of these traits (Charagu and Petrson, 1998). In contrast, when re-ranking occurs, superior individuals in one environment will be inferior in other environments. In this case, breeding organisations should face the problem of how to optimize the breeding program to respond to multiple environment requirements. When G × E exists and the environment is under the control of the breeders (i.e. genotype by ration or genetic by housing interaction), it would be easier for breeders to modify the environment to allow optimum expression of the genotype. However, when environments are beyond the breeders' control, they have to choose the genotypes able to adapt to those environments. One way to accomplish this is selection of a specific genotype for each environment. This strategy would achieve an optimum response for each environment and help maintain genetic diversity. However, it remains very costly and time consuming to have environment specific genotypes. Furthermore, under these conditions inbreeding may rise and a decline of selection response could be observed. Selection of a trait in one environment with the goal for improving the same trait in other environment known as indirect selection can also be viewed as one of the breeding strategies to address the re-ranking. The efficiency of this selection will depend on the magnitude of the genetic correlation between the two environments and the heritabilities of the trait in each of the two environments. Togashi *et al.* (2001a) reported that when sire by country interaction exists, selection of candidate animals in the country with the highest genetic variance should be more effective than selection in the country with the lowest genetic variance. Togashi *et al.* (2001b) also reported that when G × E interaction is important, an international optimum index becomes more efficient than a within country index as a means to select candidate animals. When considering only sire selection, James (1961) reported that when genetic correlation among two environments was greater than 0.70, testing progeny in both environments and applying a unique index selection was more appropriate than applying separate selection following testing in both environments or selecting and testing in only one of the two environments. Mulder (2007) concluded that a single breeding program with progeny test bulls in both environments was more appropriate when the genetic correlation was higher than 0.60. In contrast, when the genetic correlation was less than or equal to 0.60, it was more opportune to have a specific breeding program and progeny-testing in each environment.

2.7. Conclusions

This review highlights the importance of G × E in dairy cattle at the animal and breeding programs levels. Estimates of G × E interaction investigated on controlled experiments were low to zero. Advances in statistical modeling of large data sets have allowed good estimates of genetic correlations and heritabilities of traits in the discrete and the continuous environments. However, difficulties came from the "real" identification of environmental effects. Nevertheless, recent works showed good alternatives based on clustering of environments on "best-definite" descriptors. Practically, all analyses were undertaken in temperate areas with some few investigations between tropical and temperate countries. Evidence on the existence of G × E within or between countries was not clear in some cases. Many studies reported only scaling effects and a few of them reported re-ranking effects. But, nearly all these studies found G × E when differences between environments were large. In diversified intensive production systems, the cost of production, food quality, animal welfare, and consumer desires are all constraints that selection programs should consider. Information on the magnitude of G × E over different time horizons and the "best" environment identification (under favorable and harsh conditions) are needed to help the breeding decision making process. In low input systems, the best alternative to circumvent the consequences of G × E is to select for adaptive traits. This will depend on the genetic correlations between 'the import' and 'the export' environments.

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As explained in the previous chapter, studies on G x E were mainly limited to within-country analysis essentially in the northern hemisphere. Investigations on G x E effects across countries not participating in Interbull are rare. High genetic links among populations in developed countries, resulting from direct or indirect cooperation in breeding programs, are available. The very few studies that were undertaken to explore the effect of G x E between importing and exporting countries and to monitor breeding programs lacked affirmation on the existence of G x E because of the limited information available on genetic ties and pedigree depth and only a few model and/or experimental farms in the developing countries were used. This PhD thesis will use combined data from two populations known with the spread of Holsteins from continuous importation of live animals and semen from different origins. Therefore, the first investigation of the present PhD thesis was to ***evaluate the genetic relatedness between Luxembourg and Tunisian Holsteins and to measure the genetic diversity of their populations.*** *This phase was essential to verify if these two populations can be used for a G x E study. Chapter 3 describes the methodology used to investigate the genetic variability and links based on a genealogical analysis and presents afferent results. These results were compiled in a scientific paper published in the Journal of Dairy Science.*

Chapter 3

Genetic diversity and joint pedigree analysis of two importing Holstein populations

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3.1. Interpretive Summary

A genealogical analysis was performed on two Holstein populations with similar sizes but located in two continents. Measures of genetic diversity and relatedness based on contributions of major ancestors, inbreeding, and additive relationship coefficients were determined. Results show that the two populations (in Luxembourg and Tunisia) are genetically linked. The investigation of genotype by environment interactions using these two Holstein populations may be possible.

3.2. Abstract

Genetic diversity and relatedness between 2 geographically distant Holstein populations (in Luxembourg and Tunisia) were studied by pedigree analysis. These 2 populations have similar sizes and structures and are essentially importing populations. Edited pedigrees included 140,392 and 151,381 animals for Tunisia and Luxembourg, respectively. To partially account for pedigree completeness levels, a modified algorithm was used to compute inbreeding. The effective numbers of ancestors were derived from probabilities of gene origin for the 2 populations of cows born between 1990 and 2000. The 10 ancestors with the highest contributions to genetic diversity in the cow populations accounted for more than 32% of the genes. Eight of these 10 ancestors were the same in both populations. The rates of inbreeding were different in the 2 populations but were generally comparable to those found in the literature for the Holstein breed. Average inbreeding coefficients per year, estimated from the data ranged from 0.91 and 0.50 in 1990 to 3.10 and 2.12 in 2000 for the Tunisian and Luxembourg populations, respectively. Genetic links have also strengthened with time. Average additive relationships between the 2 populations were as high as 2.2% in 2000. Results suggest that it would be possible to investigate genotype by environment interactions for milk traits using the Tunisian and Luxembourg dairy populations.

Keywords: pedigree, probability of gene origin, inbreeding, genetic diversity.

3.3. Introduction

The Holstein breed is known world-wide as one of the highest yielding dairy breeds. Breeding strategies to improve milk production, based on the import of pure-bred Holstein heifers and semen have been implemented by many developed and developing countries over the last 40 years. Tunisia imported pure-bred pregnant Friesian heifers from the Netherlands in 1970 (Djemali and burger, 1992). Holsteins were then imported from Canada, the United States, and some European countries. Luxembourg has a similarly sized dairy cattle population to that of Tunisia. The Luxembourg population originally included one third red and white dairy cows. Breeders in Luxembourg like their

Tunisian counterparts imported heifers mainly from Germany. The current breeding scheme in Luxembourg is also similar to that in Tunisia. In the absence of a national progeny testing program, this scheme is based on imported semen of proven bulls with a very limited use of young sires. On the other hand, breeding goals vary between the 2 countries. In Tunisia, the focus is on increased yield by means of an intra herd index used to select cows, whereas breeders in Luxembourg rely on the RZG selection index obtained following a joint genetic evaluation with Germany. The RGZ composite index includes durability, health, and reproduction traits in addition to milk yield (Miglior *et al.*, 2005).

The intensive use of AI from a few proven sires throughout the world may result in increased levels of inbreeding. The reduced genetic diversity may hamper the success of future breeding strategies in dairy cattle. The genetic variability in a population is influenced by the number of founders, selection intensity, inbreeding, and genetic drift. Measures of genetic diversity such as effective number of founders and ancestors have recently been used to evaluate genetic variability in several species: cattle (Boichard *et al.*, 1996; Sölkner *et al.*, 1998; Roughsedge *et al.*, 1999; Honda *et al.*, 2004; Hagger, 2005), horses (Valera *et al.*, 2005), donkeys (Gutiérrez *et al.*, 2005), and dogs (Leroy *et al.*, 2006). Most of these studies were carried out using data on specific country populations; others extended their study to different breeds (Sørensen *et al.*, 2005). Investigations on dairy cattle have been based on large populations with structures involving no or little imported cattle or semen.

Genetic diversity analyses in developing countries are scarce, as are studies on genetic links among geographically distant Holstein populations. Very few studies have combined both, even if they must be addressed to investigate genotype by environment interactions and to monitor breeding programs. The objectives of this study were therefore twofold. The first objective was to measure genetic diversity for the Luxembourg and Tunisian Holstein populations given their specific situation as importing countries. The second objective was to assess genetic links between these 2 geographically distant Holstein populations.

3.4. Materials and Methods

3.4.1. Data

Tunisian data were provided by the centre for Genetic Improvement of the Livestock and Pasture Office (OEP). Original data included 102,890 pedigree records. Records were of milk recorded cows born between 1990 and 2000 (sired by 3,482 AI bulls) and their registered ancestors. Individual identity was registered following the appropriate numbering system given by the herd book of origin and contained parents and grandparents. For all animals in the original pedigree file, reference identification (**ID**) according to the international identification structure was obtained. Sire identifications were cross-checked with the Interbull cross reference files for imported bulls. Similarly, herd-book files were cross-checked for imported heifer identifications. Pedigree depth was improved by using North American pedigree files provided by the Canadian Dairy Network (Guelph, ON, Canada) and the Animal improvement Programs Laboratory (Beltsville, MD) and similar European herd-book files. The final Tunisian pedigree data included 140,392 records of animals born between 1917 and 2000. Each record included the international identification number, country of origin, birth year, sire, and dam of the animal.

Original Luxembourg pedigree data were obtained from Luxembourg Herd-book Federation (now: CONVIS–Herd-Books, Service Elevage et Génétique, Ettelbruck, Luxembourg) and were provided by United Datasystems for Animal Production [Vereinigte Informationssytem Tierhaltung (VIT), Verden, Germany]. Data included 125,134 pedigree records. Animals were identified according to an international ID. Records were of all milk recorded cows born between 1990 and 2000, along with those of their ancestors. Sire identifications were cross-checked with the Interbull cross reference files for imported bulls. As with the Tunisian data, the Luxembourg pedigree file was also improved by adding depth through the use of foreign files. The final Luxembourg data included 151,381 animals born between 1917 and 2000. Tunisian and Luxembourg files were then merged. There were 16,856 pedigree records in common, and the final pedigree used in the analysis included 259,659 animals. Figure 1 shows the evolution of records from 1941 to 2000 for both populations. The rate of registration was low before 1980. Percentages of animals registered after 1980 were 81% and 62% for Luxembourg and Tunisia, respectively.

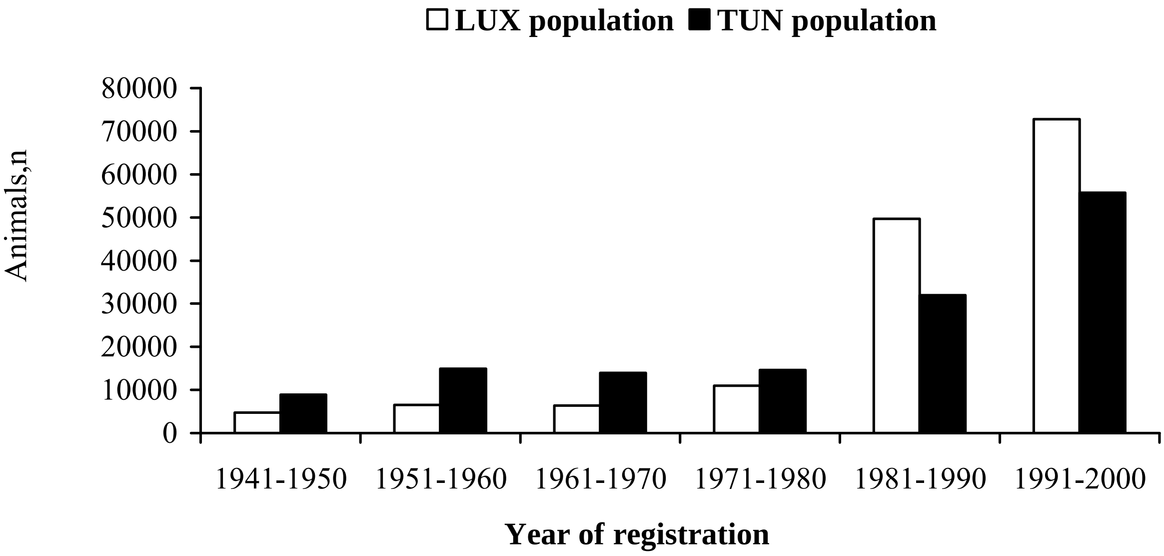

***Figure 1**. Number of registrations in Luxembourg (LUX) and Tunisian (TUN) herd books by periods of 10 yr.*

The definition of a reference population was necessary to allow comparisons. It had to be similarly defined for Luxembourg and Tunisia. This population was made up of cows with at least one test-day record and born between 1990 and 2000. Reference populations included 75,467 and 47,321 cows for Luxembourg and Tunisia, respectively. The reference period was defined to represent the last 2 generations of cows available for this study. No other edits were made. Cows in the reference populations were mainly daughters of AI bulls. The latter represent 82 and 85% of all sires registered in Tunisia and Luxembourg, respectively. These bulls were almost exclusively proven foreign sires for Tunisia (99%), whereas Luxembourg has recently used a few young bulls (8%) in addition to proven foreign ones.

3.4.2. Pedigree completeness

The pedigree completeness level was evaluated for the 2 reference populations. The fractions of known ancestors per generation were computed and the average numbers of ancestors by year of birth were traced. Updating the pedigrees led to a considerable increase in the average number of known ancestors in both populations. Cows in Luxembourg had more unknown parents than those in Tunisia. A little was gained by cross-checking with foreign files in the case of Luxembourg.

The number of known generation equivalents was then computed for each animal. This number was derived as the sum of the $(1/2)^n$ coefficients, where n is the number of generations separating animals from the known ancestor. Therefore, a parent accounts for 0.5 and a grandparent for 0.25, and so on. Finally, average numbers of known generation equivalents were obtained by birth year for the 2 reference populations. The average number of generation equivalents quantifies how many generations have been traced. After pedigree improvements, average number of known generation equivalents increased from 5.4 and 4.2 yr in 1990 to 8.2 and 6.3 yr in 2000 for the Tunisian and Luxembourg reference populations, respectively (Figure 2). Percentages of cows with unknown sires were 32% and 5% of the Luxembourg and Tunisian reference populations, respectively. Percentages of cows with unknown dams were 17 and 14%, respectively.

3.4.3. Methods

Inbreeding. To account for trends in inbreeding even when ancestors were missing, a genetic group for each animal was defined by sex, country, and birth year. Dams without pedigree records were assigned to the year of birth of their oldest progeny minus 3. Sires without pedigree records were assigned to the year of birth of their oldest progeny minus 5. The inbreeding coefficients were then computed according to the methodology described in Croquet *et al.* (2006) and based on the algorithm of Meuwissen and Luo (1992). In the method by Croquet *et al.* (2006), the estimated inbreeding coefficient of an animal with unknown origins is equal to half of the average relationship between genetic groups of its phantom parents. Average and maximum coefficients of inbreeding were computed for the populations of both countries, assuming that animals of unknown origin have inbreeding coefficients similar to the average of comparable animals. Animals were considered comparable if they were born in the same year, had the same sex, and came from the same population.

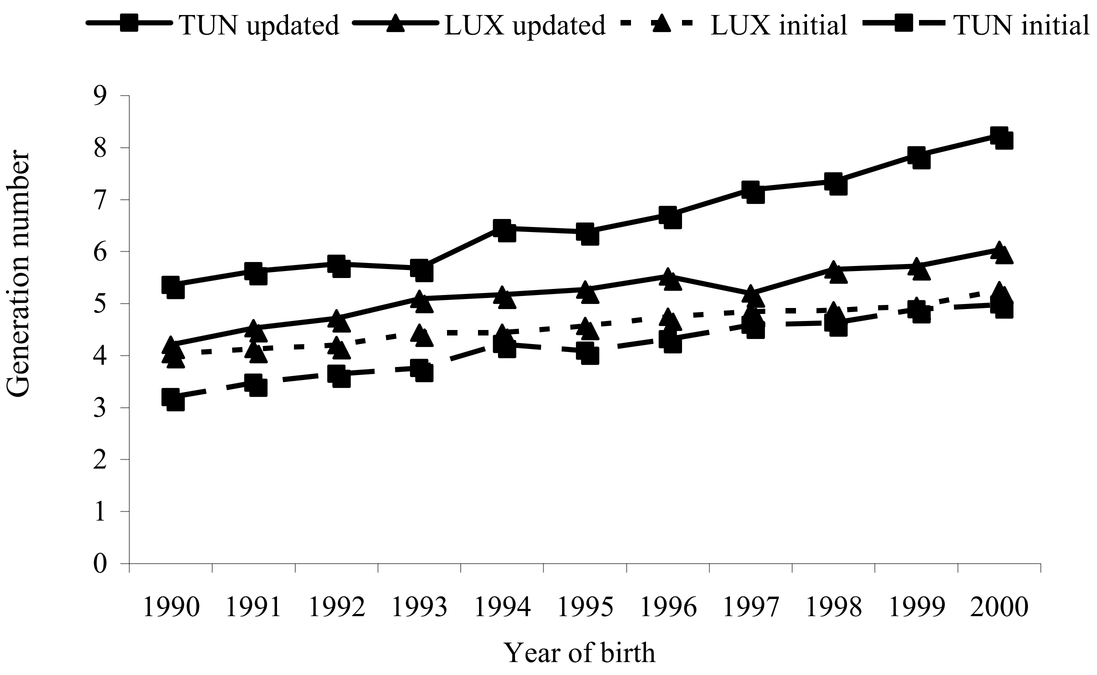

Figure 2. Average number of known generation equivalents by the year of birth for the reference populations of cows born between 1990 and 2000 in Tunisia (TUN) and Luxembourg (LUX). Initial means: pedigree as delivred by CONVIS (Convis Herdbuch, Service Elevage et Génétique, Ettelbruck, Luxembourg; LUX) and the Center for Genetic Improvement of the Livestock and Pasture Office (OEP; TUN). Updated means: edited pedigree using cross-reference files and international databases.

Effective number of founders. Each individual with unknown parents was considered as a founder. Furthermore, if an animal had one known and one unknown parent, the unknown parent was regarded as a founder. The expected genetic contribution of each founder to the reference population was defined as the probability of a gene taken at random within the reference population to come from a given founder. The genes of an animal have a 0.5 probability of originating from its sire and 0.5 probability of originating from its dam. Similarly, it has a 0.25 probability of originating from any of the animal's grandparents and so on. When this rule is applied to a population and the probabilities are accumulated by founders, each founder k is characterized by its expected contribution q_k to the gene pool of the population.

The total number of founders (**f**) in this data is expected to be very high because of missing pedigree and therefore may not fully explain genetic variability in the reference population. First, these founders are assumed to be unrelated because their parents are unknown, which is likely not the case. Second, their contributions to the reference populations may vary. Intensively used founders will contribute more to the reference population than the others. To take account for this, the effective number of founders ($\mathbf{f_e}$) was estimated. This number was defined as the number of equally contributing founders that would be expected to produce the same genetic diversity in the populations under study (Lacy, 1989). This number is given by:

$$f_e = \frac{1}{\sum_{k=1}^{f} q_k^2}$$

where f represents the number of founders and q_k is the genetic contribution of the kth founder to the reference population. When founders contribute equally, the effective number of founders is equal the total number of founders. Otherwise, the effective number of founders remains smaller than the total number of founders.

Effective number of ancestors. The effective number of ancestors was proposed by Boichard *et al.* (1997) as an alternative to the effective number of founders. It also takes into account bottlenecks in pedigrees. Ancestors here can be founders or not. The effective number of ancestors (**f_a**) represents the minimum number of equally contributing ancestors (founders or not) that are necessary to explain the complete genetic diversity in a population. The expected marginal contribution (**p_j**) of each ancestor (j) was computed as its expected genetic contribution independently of the contributions of other ancestors. The ancestor with the highest genetic contribution to the population is first chosen, and the other ancestors are selected iteratively. In the round n, the kth ancestor is chosen according to its marginal contribution (**p_k**). This latter is defined as the contribution of the kth ancestor not yet explained by the (k-1) ancestors being already chosen. Then, based on these marginal contributions, another ancestor is chosen, and so on. The effective number of ancestors is computed as:

$$f_a = \frac{1}{\sum_{k=1}^{f} p_k^2},$$

where p_k is the marginal genetic contribution of the kth ancestor not yet explained by the previous (k-1) ancestors, and f is the number of ancestors. The marginal contribution was determined for 1,000 ancestors in this study. The number of ancestors with a positive marginal genetic contribution is less than or equal to the total number of founders. The effective number of ancestors is more accurate than the effective number of founders to measure genetic diversity. The classic and simple approach for estimating the effective number of founders overestimates the former when the pedigree is undergoing a bottleneck. Let us consider an example in which the reference population is simply a set of full-sibs from 2 unrelated parents. When the grandparents are considered, the effective number of founders computed is 4, and is multiplied by 2 for each additional traced generation, whereas the effective number of ancestors is 2 (the 2 parents). This overestimation is particularly important when the germplasm of a limited number of breeding animals is widely spread, which is the case of the 2 populations in this study because of the intensive use of a few AI bulls. The effective number of ancestors takes into account the most recent bottlenecks. However, it should be used in parallel with the effective number of founders. The effective number of ancestors does not take into account the probabilities of gene losses by drift.

Relatedness between populations. The additive genetic relationship coefficients within and between Tunisian and Luxembourg female reference populations were calculated following the algorithm by Boichard *et al.* (2002). This algorithm builds up the relationship matrix, term by term, by generating a progeny for each combination from which the inbreeding coefficient was derived following the method of Meuwissen and Luo (1992). Pair-wise genetic relationship coefficients between sires used in the 2 reference populations were also estimated. Furthermore, an average genetic relationship coefficient between proven bulls born in 1995 and originating from various Interbull country members and living females during 1999 in Luxembourg and in Tunisia was obtained. The birth year of 1995 was chosen to hypothetically suggest that bulls born in 1995 could be potential sires of cows born in 1999 in Tunisia and Luxembourg.

Finally, the genetic similarity (**GS**) between the Luxembourg and Tunisian cow populations was computed following Rekaya *et al.* (2003). Genetic similarity was defined as the ratio of the number of daughters of common bulls to that of all bulls:

$$GS(i,j) = \sum_{r=1}^{2} \sum_{k=1}^{C(i,j)} ND_{kr} \bigg/ \sum_{r=1}^{2} \sum_{k=1}^{T(i,j)} ND_{kr} \ ,$$

where C(i,j) is the number of bulls in common used in country i and j, T(i,j) is the total number of bulls used in both countries, and ND_{kr} is the number of daughters of bull k in country r (r=1,2).

3.5. Results

The effective number of founders (f_e) differed between the 2 reference populations (Table 1) for the 1990 to 2000 period. This number was higher for the Luxembourg population than the Tunisian population. The effective number of ancestors was smaller than that of founders. The former was also lower in the Tunisian than in the Luxembourg population. The effective numbers of founders were 112 and 295 for the Tunisian and Luxembourg Holstein populations in 2000, respectively. These effective founders corresponded to 22 and 44 effective ancestors, respectively (Table 1). From 1990 until 2000, the effective numbers of ancestors decreased by almost 60% in both countries.

Total numbers of ancestors contributing 50% of the gene pool were low and tended to decrease from 1990 to 2000 in both countries. Cumulative marginal contributions of ancestors showed similar patterns in both populations (Figure 3). A small number of ancestors contributed heavily to the reference populations, whereas the rest of the genes came from a great number of ancestors with low marginal contributions.

***Table 1**. Numbers of founders and ancestors for the Tunisian and Luxembourg populations of cows born between 1990 and 2000*

Country	1990	1992	1994	1996	1998	2000
	Total number of founders					
Luxembourg	9,089	9,111	9,231	9,261	9,522	9,328
Tunisia	8,949	10,386	10,458	10,936	12,196	10,794
	Effective number of founders					
Luxembourg	373	387	332	313	305	295
Tunisia	194	194	153	136	123	112
	Effective number of ancestors					
Luxembourg	97	75	55	50	47	44
Tunisia	49	46	33	29	28	22
	Number of ancestors accounting for 50% of the gene pool					
Luxembourg	57	57	46	31	26	24
Tunisia	34	26	19	15	13	9

Birth year spans columns 1990–2000.

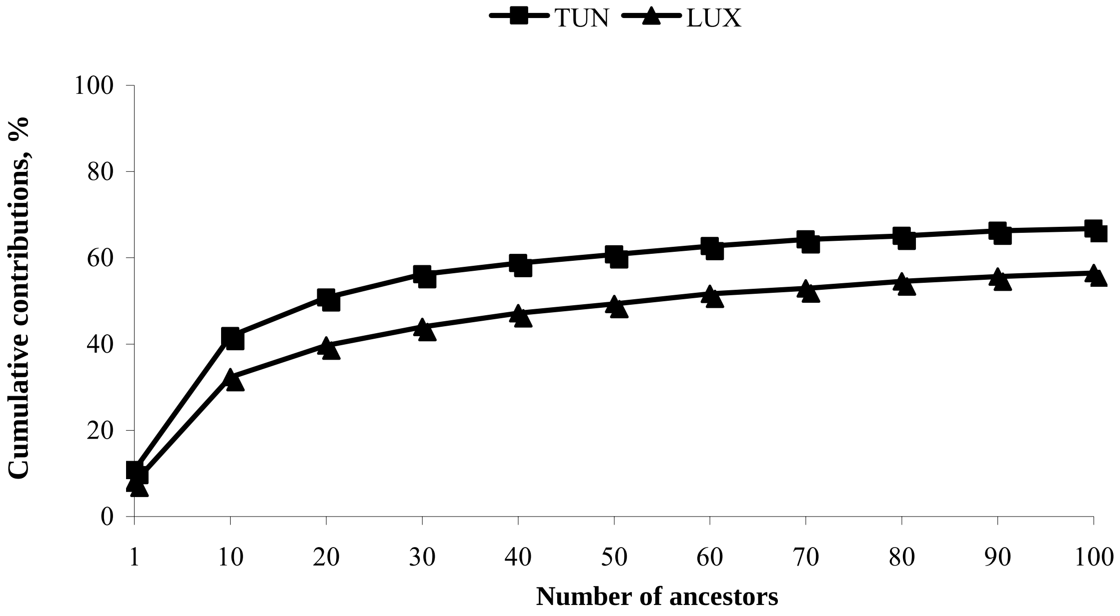

***Figure 3**. Cumulative marginal genetic contributions of ancestors to the Tunisian (TUN) and Luxembourg (LUX) Holstein populations.*

The most popular ancestors with the largest marginal contributions to the reference populations (33% in Luxembourg and 42% in Tunisia) are given in Table 2. It is interesting to notice that the 10 most important ancestors of Luxembourg Holsteins explained approximately 40% of the genetic diversity in the Tunisian female population. The specific presence of Hannover Hill Triple Threat in Luxembourg can be explained by the fact that this sire was specifically used in Red Holstein populations and that the Luxembourg dairy cattle population had historically one third red and white cows.

Inbreeding trends for females raised in Luxembourg and in Tunisia between 1990 and 2000 are shown in Figure 4. Inbreeding levels prior to 1990 (not given) were low in both countries and varied from 0.042 and 0.04% in 1983 to 0.97 and 0.3% in 1989 for the Tunisian and Luxembourg populations, respectively. The level of inbreeding observed for the Tunisian reference population (3.10%) was higher than that observed for the Luxembourg population (2.12%). Differences between average inbreeding coefficients of Luxembourg and Tunisian populations doubled from 1990 to 2000.

***Table 2**. Marginal genetic contributions (%) to the Luxembourg and Tunisian cow populations by the most popular ancestors ranked on their contributions to the Luxembourg population*

Ancestor	Luxembourg		Tunisia	
	Rank	Contribution (%)	Rank	Contribution (%)
Round Oak Rag Apple Elevation	1	7.87	2	10.35
Pawnee Farm Arlinda Chief	2	5.73	1	10.70
Osborndale Ivanhaoe	3	3.46	3	4.95
Hanover-Hill Triple Threat	4	3.21	(> 1000)	(< 0.01)
Paclamar Astronaut	5	3.04	6	2.42
Dam of SWD Valiant	6	2.64	5	3.18
ABC Reflection Sovereign	7	2.19	9	1.55
Carlin-M Ivanhaoe Bell	8	1.74	4	3.38
Wisconsin Admiral Burke Lad	9	1.4	(33)	(0.3)
No-Na-Me Fond Matt	10	1.07	7	2.15
Paclamar Bootmaker	(26)	(0.42)	10	1.35
Whittier-Farms Ned Boy	(> 1000)	(< 0.01)	8	1.83
Total contribution		32.35		41.86

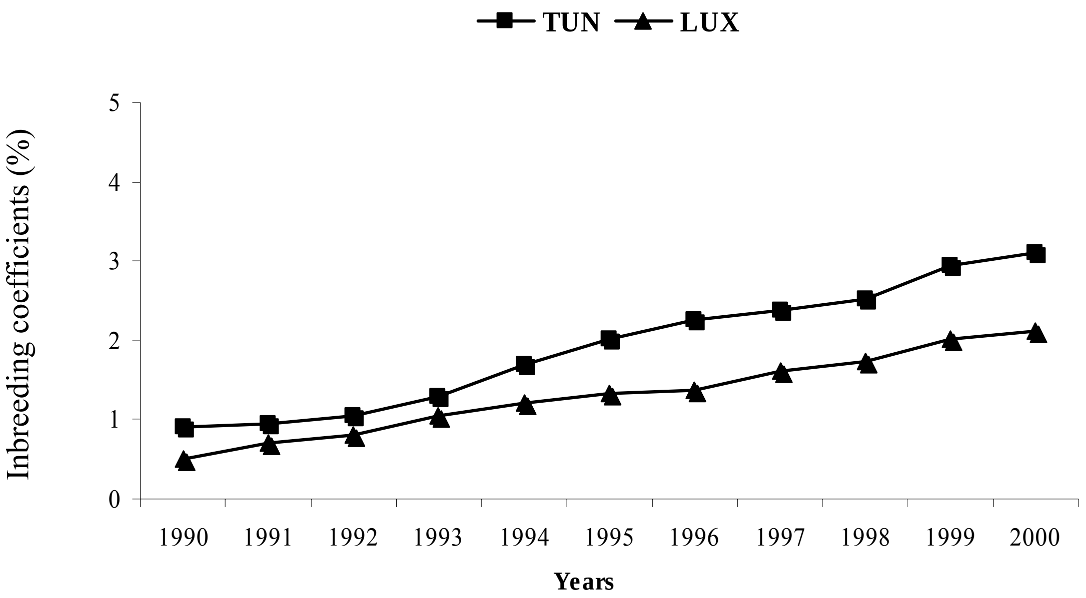

***Figure 4**. Inbreeding trends for Tunisian (TUN) and Luxembourg (LUX) Holstein female populations.*

Averages of pair-wise genetic relationship coefficients are shown in Figure 5. Curves illustrating the rates of change in additive relationships within each population were steeper than those of inbreeding trends. Additive relationships in the Tunisian reference female population increased by approximately 0.25% each year. Relationship coefficients within the Tunisian reference population were higher than those found within the Luxembourg population. The build up of additive relations was also slower within the Luxembourg female population.

Average pair-wise relationships between the sires of cows born in Tunisia and Luxembourg between 1990 and 2000 (Table 3) were greater than those between their daughters (Figure 5). There is a considerable variation in relationship levels among sires used in the 2 countries during the 11 yr of the study (SD > 3%). The proportion of sires with less than 1% relationship coefficients decreased from one year to another, whereas that of sires with more than 6% relationship coefficients did increase.

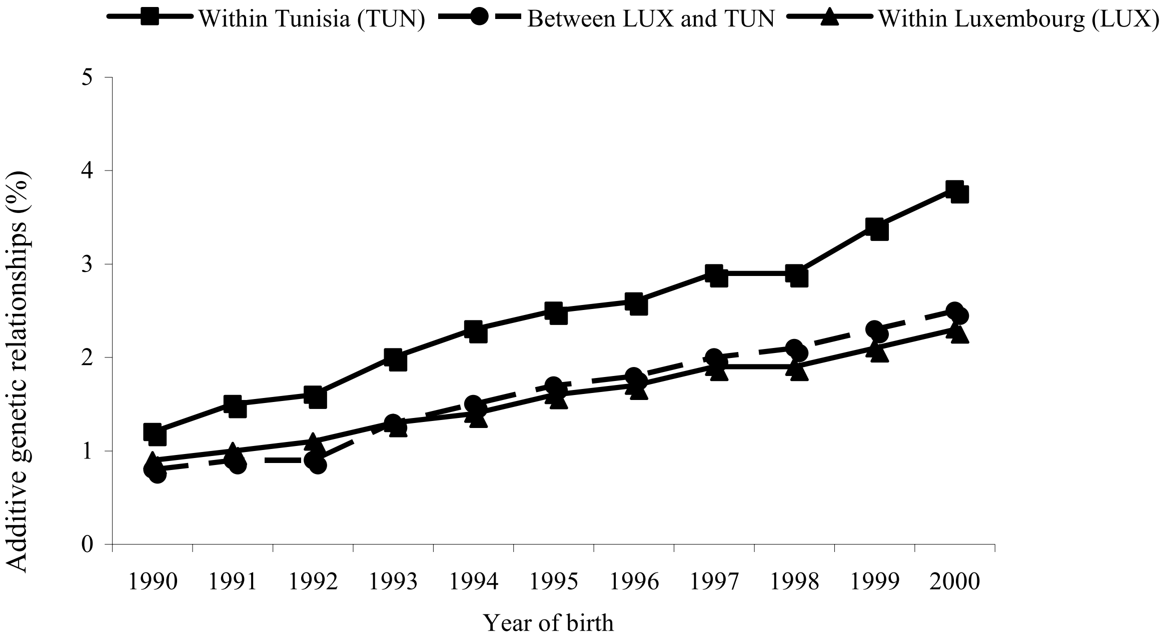

Figure 5*. Average pair-wise additive relationships within and between Luxembourg (LUX) and Tunisian (TUN) Holstein cows born between 1990 and 2000.*

Table 3*. Average pair-wise relationship (AR) between sires of cows born from 1990 to 2000 in Luxembourg and in Tunisia*

Birth year of cows	Average relationship, (%)	SD, (%)	Percentage of sires with AR <= 1%	Percentage of sires with AR >= 6%
1990	2.4	2.8	39	10
1991	2.9	3.2	34	14
1992	3.0	3.3	33	15
1993	3.1	3.2	30	14
1994	3.2	3.1	23	14
1995	3.7	3.2	18	16
1996	3.9	3.2	15	16
1997	4.3	3.4	11	20
1998	4.3	3.3	8	20
1999	4.5	3.4	9	22
2000	4.7	3.4	6	24

Estimates of genetic similarities between the Luxembourg and Tunisian Holstein populations are given in Table 4. The percentage of daughters, having test-day records and sired by common bulls in Luxembourg and Tunisia represented 15 and 13%, respectively, of the total females registered in each population. The number of common sires with daughters having milk records in each of the 2 countries was 262.

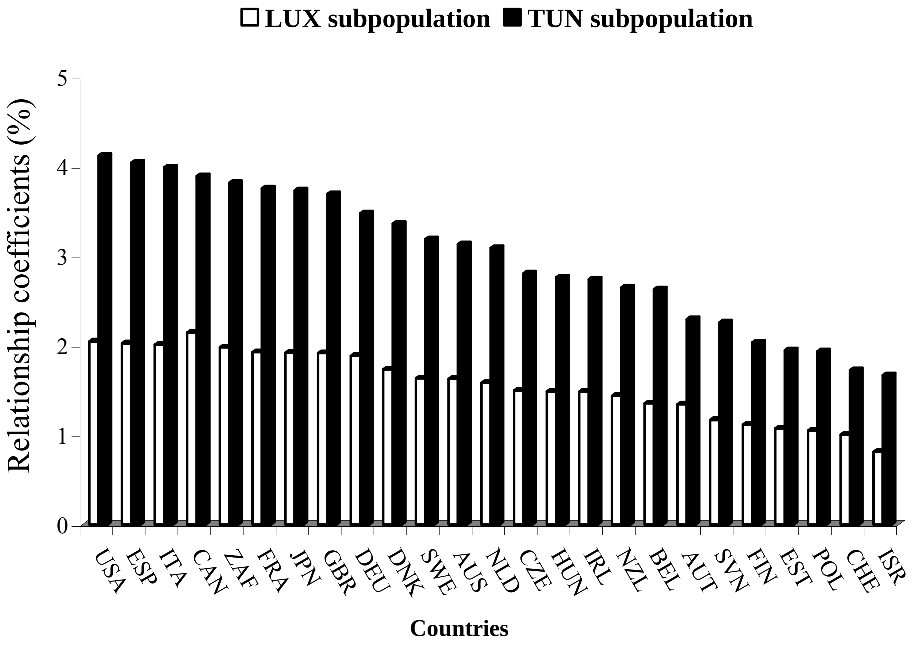

***Figure 6**. Average relationships between females living in 1999, in Luxembourg (LUX) and Tunisia (TUN) in 1999, and tested bulls in Interbull country members born in 1995. USA= United States; ESP = Spain; ITA = Italy; CAN = Canada; ZAF = Republic of South Africa; FRA = France; JPN = Japan; GBR = Great Britain; DEU = Germany; DNK = Denmark; SWE = Sweden; AUS = Australia; NLD = the Netherlands; CZE = Czech Republic; HUN = Hungary; IRL = Ireland; NZL = New Zealand; BEL = Belgium; AUT = Austria; SVN = Slovenia; FIN = Finland; EST = Estonia; POL = Poland; CHE = Switzerland; ISR = Israel.*

***Table 4**. Genetic links between the Luxembourg and Tunisian Holstein populations*

Sires with daughters having test day yields in the 2 countries			Total common sires in the whole pedigree	Genetic similarity
% of all cows		No. of sires		
Luxembourg	Tunisia			
14.9	13.2	262	2286	0.19

3.6. Discussion

The present study exemplifies the effects of the Holstein gene flow on the Luxembourg and Tunisian cattle populations. It illustrates the extent to which geographically distinct populations can be genetically related as a result of the extensive use of AI. Inbreeding levels in this study are comparable to those reported for most other Holstein populations (Boichard *et al.*, 1996; Young and Seykora, 1996; Sørensen *et al.*, 2005). The level of inbreeding observed for the Luxembourg reference population was comparable to those reported for the Irish (McParland *et al.*, 2007) and UK (Kearney *et al.*, 2004) Holstein populations. However, the level of inbreeding found for the Tunisian population was lower than that reported for the Canadian Holsteins (> 4%) in the same period (Van Doormaal *et al.*, 2005). The increase in inbreeding was nearly linear, at rates of 0.23 and 0.15% per year for the Tunisian and Luxembourg populations, respectively. Kearney *et al.*, (2004) reported a rate of 0.17% per year for the UK Holstein population for the same period. The high level of inbreeding observed in Tunisia can at least partially be explained by the use of fewer and more related sires per breeding season. Daughter group sizes per sire (Table 5) have been much larger in Tunisia than in Luxembourg in recent years.

Table 5. *Daughter group sizes and average relationships (AR) among their sires for the reference populations of cows born between 1990 and 2000 in Tunisia and in Luxembourg*

Year of birth	Average number of daughters / sire		Maximum number of daughters /sire		AR among their sires (%)	
	Tunisia	Luxembourg	Tunisia	Luxembourg	Tunisia	Luxembourg
1990	7	9	487	188	2.01	0.95
1991	7	9	210	215	2.04	1.08
1992	7	8	272	290	2.10	1.18
1993	7	8	314	225	2.17	1.35
1994	8	9	331	355	2.74	1.43
1995	7	9	338	295	2.76	1.53
1996	7	9	200	203	2.93	1.65
1997	10	7	300	122	3.41	1.64
1998	8	9	278	209	3.47	1.79
1999	15	9	393	216	4.05	1.83
2000	14	9	274	172	4.41	1.98

In fact, the average number of daughters per sire in Tunisia actually increased 2-fold between 1990 and 1997 compared to a nearly constant number of daughters per sire during the same period in Luxembourg. Average daughter group sizes per sire, as shown in Table 5, were relatively low in both countries, as expected by the small size of both populations. The reported average inbreeding level in Luxembourg in this study was lower than that found in Tunisia. Probably this is due to its lower pedigree completeness and also to the important non-Holstein contribution of the Maas-Rhine-Yssel type Red and White animals to the original gene pool. In fact, historically around one-third of the cattle population in Luxembourg was Maas-Rhine-Yssel type Red and White animals. This source of genetic diversity has been eroded by the massive use of pure-bred Red Holstein sires since the 1980's.

Measures based on probabilities of gene origin used to evaluate genetic diversity in the Luxembourg and Tunisian reference populations show that both populations are derived from small numbers of founding animals. The effective numbers of founders and ancestors for the Luxembourg population were slightly higher than those obtained for the Tunisian population, indicating that the number of animals contributing to the gene pool was low in the case of the Tunisian population. The total numbers of founders (in Tunisia and in Luxembourg) were high in this study because of missing pedigree information (an animal was regarded as a founder if its parents are declared unknown). A low ratio of the effective number of founders to the total number of founders (**f**) implies an unbalanced use of founders, missing pedigree information, or both. Indeed, a substantial disequilibrium was found for the 2 populations. The ratio f_e/f was 0.02 and 0.04 in 2000 for Tunisia and Luxembourg, respectively. Nevertheless, the ratios found in this study are higher than the 0.002 found in Irish Frisiean Holsteins (McParland *et al.*, 2007) and also to the 0.0002 reported for French Holsteins (Boichard *et al.*, 1996). These results show that ratios f_e/f can only be compared for populations that have a similar size. However, the ratio f_e/f in 2000 for Tunisia was still similar to those found in Austrian Brown Swiss populations (0.016; Sölkner *et al.*, 1998) and the French Tarentais populations (0.017; Boichard *et al.*, 1996).

The effective number of ancestors (founders or not) is the parameter most affected by the quality of pedigrees (Boichard *et al.*, 1997). Estimates of effective number of ancestors of female populations born in 2000 were 44 and 22 from the Luxembourg and Tunisian data, respectively. In Tunisian Holsteins, this parameter was similar to the value (20.6) reported by Sørensen *et al.* (2005) for the Danish Holsteins, but was still lower than the value (93) found for the British Holstein-Friesian population (Roughsedge *et al.*, 1999). The British results may be explained by a still relatively important influence of British Friesians in 1999. The effective number of ancestors for the Luxembourg population was similar to the value (43) reported by Boichard *et al.*, (1996) for the French Holsteins.

The comparison between the effective number of founders and the effective number of ancestors reveals the reduction of the genetic variability in populations that have passed through bottlenecks (Boichard *et al.* 1997). Effective numbers of ancestors were lower than effective numbers of founders in both populations of the study. The ratios f_a/f_e were 0.15 and 0.19 in 2000 for the Luxembourg and Tunisian populations, respectively. These ratios are lower than 0.30 for the French Holstein (Boichard *et al.*, 1996) and 0.29 for the Danish Holstein (Sørensen *et al.*, 2005) populations. Despite a larger total number of founders in the Tunisian population, its effective numbers of founders and of ancestors were smaller than those of the Luxembourg population (Table 1). These observed numbers show that the expected contributions of founders, ancestors, or both were more unbalanced in the Tunisian than in the Luxembourg population. This can be partially explained by differences in pedigree depths between the 2 populations and by the contribution of the Maas-Rhine-Yssel type Red and White animals to the Luxembourg gene pool.

Average additive relationship coefficients between the 2 female reference populations were smaller than the Tunisian relationship coefficients but were comparable to those of the Luxembourg population. Percentages of females with known parents represented 86 and 64% of the Tunisian and Luxembourg reference populations, respectively. The average genetic relationship among Tunisian females born between 1993 and 1996 was comparable to the 2.2% found in the same period between French Holstein cows (Moureaux *et al.*, 2003). Links among the Luxembourg and Tunisian populations seem to be essentially due to the use of semen from bulls with common ancestors. These 2 populations share the same major ancestors. Eight out of the 10 most important ancestors were common for the 2 reference populations. Seven of them were also found among the 10 most important contributors to Danish Holsteins (Sørensen *et al.*, 2005), with genetic contributions comparable to those found for the Tunisian reference population. The 2 top ranked contributors to Danish Holsteins were Round Oak Rag Apple Elevation with 13.8% and Pawnee Farm Arlinda Chief with 10.9%. Thus far, these same sires have contributed, respectively, 10.35 and 10.7% to the Tunisian population. Together, Elevation and Chief contributed 13.6 and 21% to the Luxembourg and Tunisian reference populations, respectively. They are also the same most contributing ancestors to the American Holstein populations (Young and Seykora, 1996). Genetic links between the Luxembourg and Tunisian populations can also be explained by Tunisian pregnant heifer imports from Germany between 1993 and 2000. In fact, Luxembourg ancestors have close links with the German population. Almost half of the Luxembourg ancestors originate from Germany and the Netherlands (34.5 and 13%, respectively), although only 6 and 2.5% of Tunisian ancestors are from Germany and the Netherlands, respectively. The Tunisian and Luxembourg Holstein reference populations share almost the same proportion of ancestors originating from Canada (12.5 and 13.5% of the total ancestors, respectively). On the other hand, the Tunisian Holstein population has a higher number of genes originating from the US Holstein (71.5% of ancestors) than the Luxembourg population (38.5% of ancestors).

Additive relationships obtained among sires used by the 2 reference populations were higher than those obtained among females in both countries. Similar results were found inside the French Holstein population (Moureaux *et al.*, 2003) where average additive relationships among AI sires born between 1991 and 1995 were 2 times higher than those obtained among females born between 1993 and 1996. Genetic relationships among sires used in Luxembourg and in Tunisia result from the use of a limited number of Holstein sires. Van Doormaal *et al.*, (2005) reported that Elevation (the most contributing ancestor to the Luxembourg and Tunisian Holstein reference population) had at least 94% of the 1999-born proven sires as descendants in 11 of the 13 important Interbull countries. The 1999 female sub-populations defined for both countries were related to exactly the same group of bulls in Interbull countries. Only a difference in the level of the relationship was observed, which might be explained by the presence of red ancestors in the Luxembourg Holstein population. Except for a difference in the level of genetic relationships values, Van Doormaal *et al.*, (2005) also found that the Canadian Holstein population born in 2004 was related in a very similar fashion to 1999-proven bulls in Interbull countries. From their analysis, the proven bulls from Canada, Spain, Japan, Italy and United States had the highest percentage of genes in common with the Canadian Holstein population born in 2004, with a genetic relationships value of more than 9%. Proven bulls born in

Australia, Ireland, New Zealand and Poland were those with the smallest additive relationship to Canadian Holstein heifers born in 2004. A similar result was found for Luxembourg and Tunisian populations in this study.

Measures of the genetic similarity asserted the presence of genetic links between the Luxembourg and Tunisian populations. These links are, for example, greater than those reported between the Nordic Holstein and Ayrshire populations (Pedersen *et al.*, 2001). Proportions of daughters with common sires were 14.9 and 13.2% of all cows in Luxembourg and in Tunisia, respectively (Table 4). Corresponding proportions were only 2.8 and 2.3% in Swedish and Finnish Holstein populations, and 10.0 and 1.3% in Danish and Finnish Holstein populations, respectively. The Swedish and Danish Holsteins are more connected, and the respective proportions of daughters with common sires in these 2 populations were 10.2 and 20.7%.

The results of this study allowed the genetic structure of the Holstein breed in Tunisia and Luxembourg to be characterized. Breeding schemes are based on semen and some heifer imports in both countries. In Tunisia, breeding decisions are based on recorded yield or an intra-herd index for cows, and essentially on a milk yield index for AI bulls. However, breeding decisions do not take into account traits other than milk yield, such as fertility, longevity, and morphology. The inclusion of these traits in breeding goals could allow the use of other bulls, and consequently the enrichment of the gene pool, as has been the case in Luxembourg in recent years. The average relatedness parameter (VanRaden and Smith, 1999) could be a means to monitor genetic variability and to plan mating. However, there should be greater efforts to enhance pedigree recording of Tunisian and Luxembourg cattle populations for an appropriate monitoring of genetic variability.

3.7. Conclusions

Pedigrees of the Luxembourg and Tunisian Holstein populations were analyzed simultaneously. Pedigree completeness level was partial in both populations. Rates of change in inbreeding were 0.23 and 0.15% per year between 1990 and 2000 for the Tunisian and Luxembourg populations, respectively. Respective inbreeding levels were up to 3.10 and 2.12% in 2000. Inbreeding estimates from the Luxembourg data were lower than those from the Tunisian data, probably because of a relatively greater diversity of gene origin in the Luxembourg population and lower pedigree completeness. Furthermore, breeders from Luxembourg used a few young bulls in recent years.

Average additive relationship coefficients and genetic similarity have also increased indicating that indirect genetic links have been developing between the 2 populations. Average additive relationships between the 2 populations were greater than 2% in 2000. The 2 populations considered in this study have close genetic links that may allow studies of genotype by environment interactions.

The use of new bulls is recommended in both populations for the enrichment of the gene pool. Breeding plans should focus on genetic gain maximization and also on the maintenance of genetic diversity. Mating plans involve having knowledge of genealogical affiliation of candidate animals. Therefore, there should be greater efforts to enhance pedigree recording of the Tunisian and Luxembourg cattle populations.

3.8. Acknowledgments

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The previous chapter focused on genetic variability and relationships between Luxembourg and Tunisian Holsteins that have performance data recorded in a periode over the last 10 years. Results suggested that the Holstein genes were intensively introduced into these two populations and that genetic relationships and similarities strengthened with time among them. As the two populations considered in this study had close genetic links, G x E interactions can be studied. However to do this, specific models are need to do the genetic evaluation of animals. These models required first the estimation of genetic parameters of production traits for the studied populations. Currently, genetic evaluations for dairy cattle are performed in most countries using TD models rather than traditional lactation models. When extended to random regression TD models, they allow a better differentiation of the shape of the lactation curve of a cow. Given the correlation between milk yield and its components, a multitrait analysis that includes milk, fat, and protein yields allows records on milk yield to contribute to the accuracy of evaluations of fat and protein yields. This characteristic has efficient practical outcomes essentially when records on milk components are missing or less frequent. In Tunisia as in most of low-input systems, milk recording data are generally scarce, costly to obtain for smallholders and missing data are frequent. Thus, the use of multitrait random regression TD models may be suitable to overcome these shortcomings. Therefore, the second part of this thesis focused on ***the estimation of genetic parameters for Tunisian Holsteins based on a multi-trait-multi-lactation random regression TD model towards the implementation of a genetic evaluation model****. Chapter 4 details the proposed model and summarizes results published in Journal of Dairy Science.*

Chapter 4

Genetic Parameters for Tunisian Holsteins using a Test-Day Random Regression Model

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4.1. Interpretive Summary

Genetic parameters for milk, fat, and protein yields were estimated for the first three lactations using a three-trait-three-lactation random regression model. The estimated heritabilities, which were low, could reflect unsatisfactory management conditions of Holsteins in Tunisia. Results may serve as a first step towards implementation of a routine national genetic evaluation, which is required for selection of animals appropriate for local circumstances.

4.2. Abstract

Genetic parameters of milk, fat, and protein yields were estimated in the first 3 lactations for registered Tunisian Holsteins. Data included 140,187; 97,404; and 62,221 test-day production records collected on 22,538, 15,257, and 9,722 first-, second-, and third- parity cows, respectively. Records were of cows calving from 1992 to 2004 in 96 herds. (Co)variance components were estimated by Bayesian methods and a 3-trait-3-lactation random regression model. Gibbs sampling was used to obtain posterior distributions. The model included herd x test-date, age x season of calving x stage of lactation [classes of 25 DIM], production sector x stage of lactation (classes of 5 DIM) as fixed effects and random regression coefficients for additive genetic, permanent environmental, and herd-year of calving effects, which were defined as modified constant, linear, and quadratic Legendre coefficients. Heritability estimates for 305-d milk, fat, and protein yields were moderate (0.12 to 0.18) and in the same range of parameters estimated in management systems with low to medium production levels. Heritabilities of TD milk and protein yields for selected DIM were higher in the middle than at the beginning or the end of lactation. Inversely, heritabilities of fat yield were high at the peripheries of lactation. Genetic correlations among 305-d yield traits ranged from 0.50 to 0.86. The largest genetic correlation was observed between the first and second lactation, potentially due to the limited expression of genetic potential of superior cows in later lactations. Results suggested a lack of adaptation under the local management and climatic conditions. Results should be useful to implement a BLUP evaluation for the Tunisian cow population; however, results also indicated that further research focused on data quality might be needed.

Keywords: genetic parameters, random regression model, test-day yields, dairy cattle.

4.3. Introduction

The use of test-day (**TD**) models to analyze milk production data has several advantages over the use of lactation models. TD models account for environmental factors that could affect the performance of cows throughout the lactation (Ptak and Schaeffer, 1993;

VanRaden, 1997). Also, no extension of incomplete lactations is needed, and TD models are better suited to predict daily production, to detect outliers, and, consequently, to help decision making for management purposes (Mayeres *et al.*, 2004). TD models use larger data sets, however, and usually require estimates of more parameters than a lactation model. However, they facilitate the use of information from ongoing operations, the inclusion of data from different recording schemes by weighing every TD accordingly, and the use of data with missing milk components at given TD if used in a multivariate analysis.

Genetic parameters of TD milk traits using random regression (**RR**) models have been reported for several cow populations from fitting various functions to model additive genetic lactation curves (Jamrozik and Schaeffer, 1997; Strabel and Mizstal, 1999; Jakobsen *et al.*, 2002; Druet *et al.*, 2003; Strabel *et al.*, 2005; Muir *et al.*, 2007). Legendre orthogonal polynomials seem to efficiently describe the evolution of milk yields during a complete lactation of dairy cows in different management conditions (Rekaya *et al.*, 1999; Gengler *et al.*, 1999; Brotherstone *et al.*, 2000). Recently, RR models applied to TD records have been implemented by most Interbull members for the evaluation of dairy populations.

The size of the Holstein cow population has substantially increased over the recent years in Tunisia through the import of pregnant heifers and semen from temperate countries. Most cows are daughters of sires with strong genetic links to the United States, Canadian, and some European populations (Hammami *et al.*, 2007). In 2000, Holsteins accounted for more than 40% of the 455,000 total cows in Tunisia. Cows enrolled in the A4 official milk recording system (since the 1960s) were about 10% of the total Holstein population in 2000 (Rekik *et al.*, 2003). Alternate and owner farm recording systems are being encouraged to increase the number of Holstein cows enrolled in the national milk recording system. Unfortunately, the data generated by the milk recording is currently not sufficiently and adequately used, especially because of the lack of a genetic evaluation. Replacements and culling operate only on an intra-herd index for milk yield. Milk components are rarely considered in making breeding decisions. Selection of candidate animals should, however, be made on EBV to improve milk production under local conditions. Prediction of BLUP breeding values requires estimates of variance components. The implementation of a TD model for the genetic evaluation of milk traits using a RR model, as done by most Interbull countries, requires genetic parameters under Tunisian conditions. Tunisia has been a member of the International Committee for Animal Recording and Interbull since 1980; however, full participation of Tunisia in these organizations requires a genetic evaluation system.

The objective of this study was, therefore, to estimate (co)variance components of milk, fat, and protein yields in the first 3 lactations with a RR model by using Bayesian methods and Gibbs sampling. This study was a first step towards a Tunisian genetic evaluation system for yield traits based on a TD model.

4.4. Materials and Methods

4.4.1. Data

Data were provided by the Tunisian Genetic Improvement Center, Livestock and Pasture Office, Tunis. Original data from the official milk recording data base included 1,321,782 TD records collected on cows calving from 1992 to 2004. The number of herds enrolled in the milk recording plan has been increasing since the 1990s. For this reason, not all cows were in their first lactation when they were first enrolled in a recording system. Furthermore, the numbers of TD records for milk, fat, and protein yields were not equal, because fat and protein yields were missing in some TD due to technical reasons. In this study, only records from the first 3 lactations were retained. All third-lactation cows were required to have first- and second-lactation records. Likewise, second-lactation cows had first-lactation records. A minimum of 5 TD records, for milk, fat, and protein yields were required for a cow observation to be included in the analysis, which excluded cows with very short lactations. Records obtained before 5 or after 330 DIM were also discarded. TD records up to 330 DIM were kept to improve modeling lactation curves around 305 DIM. Herds with fewer than 4 cows per herd x year of calving were omitted. Further edits excluded irregular data for daily milk yield (< 1.0 and > 70 kg), fat content (< 1.5% and > 9%), and protein percentage (< 1% and >7%). Edited data included 140,187; 97,404; and 62,221 TD records collected on 22,538; 15,257; and 9,722 first-, second-, and third-lactation cows that were daughters of 1,720; 1,461; and 1,219 sires, respectively. Lactations had to start between 22 and 45 mo, 32 and 65 mo, and 42 and 80 mo of age for the first-, second-, and third-lactation cows, respectively.

Four seasons (fall, winter, spring, and summer), and 6 subclasses for age at calving for the first lactation (< 26 mo, 26 to 27, 28 to 29, 30 to 31, 32 to 33, and > 33 mo), 4 classes for the second lactation (< 40 mo, 40 to 42, 43 to 45, and > 45 mo), and 3 classes for the third lactation (< 54 mo, 54 to 58, and > 58 mo) were defined. Four production sectors (state, cooperative, commercial and private farms) were defined, because large management differences exist among these types of farms. A full description of the data used is given in Table 1.

4.4.2. Analysis

Data were analyzed with a 3-trait-3-lactation RR TD model. The matrix notation of the model is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}(\mathbf{Za} + \mathbf{Zp} + \mathbf{Wh}) + \mathbf{e},$$

where **y** = a vector of milk, fat and protein yields**;** **b** = a vector of the fixed effects: herd x test-date, age x season of calving x classes of 25 DIM, and sector of production x classes of 5 DIM (nested within parities); **p** = a vector of RR coefficients for permanent environmental (**PE**) effect; **a =** a vector of RR coefficients for animal genetic (**AG**) effect; **h** = a vector of RR coefficients for herd-year of calving common environmental effect

(**HY**); **e** = a vector of residual effects; **Q** = a matrix of 3 modified Legendre polynomials (constant, linear, quadratic) as defined by Gengler *et al.* (1999); and **X**, **Z,** and **W** = incidence matrices relating observations to various effects. The covariance structure of the model is:

$$V\begin{bmatrix}\mathbf{a}\\\mathbf{p}\\\mathbf{h}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{K_a} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\\mathbf{0} & \mathbf{I}\otimes\mathbf{K_p} & \mathbf{0} & \mathbf{0}\\\mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\mathbf{K_h} & \mathbf{0}\\\mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix}$$

where $\mathbf{K_a}$ = the 27 × 27 covariance matrix of the AG regression coefficients; **A** = the AG covariance matrix among all animals; $\mathbf{K_p}$ = the 27 × 27 covariance matrix of the PE regression coefficients; $\mathbf{K_h}$ = the 27 × 27 covariance matrix of the HY regression coefficients, and **R** = a 9 × 9 diagonal matrix of residual variances.

Variance components were estimated with a Bayesian approach via the Gibbs sampling algorithm as implemented by Misztal *et al.* (2002). Posterior means of variance components, heritability, and correlation estimates were obtained using 100,000 samples after a burn-in of 20,000 samples. Convergence of Gibbs chains was monitored by inspection of plots related to selected parameters.

The genetic variance matrix among all DIM and traits was obtained following Druet *et al.* (2003), as $\mathbf{G}=\mathbf{Q}\mathbf{K}_a\mathbf{Q}'$ where **G** = a 9 × 330 by 9 × 330 genetic (co)variance matrix for all 9 traits and DIM ranging from 1 to 330 d and **Q** = a 9 × 330 by 27 matrix with the values of the 9 coefficients of the third order Legendre polynomial for each DIM from 1 to 330 d for every trait. The PE and HY effect (co)variance matrices were similarly defined and **P** and **H** matrices were estimated from the $\mathbf{K}_p$ and $\mathbf{K}_h$.matrices.

Genetic (co)variances for 305-d yields were obtained by using $\mathbf{G}_{\text{lact}}=\mathbf{S}\mathbf{G}_{305}\mathbf{S}'$ where $\mathbf{G}_{\text{lact}}$ = the 9 × 9 (co)variance matrices among 305-d lactation yields for the 9 traits, $\mathbf{G}_{305}$ = a partial matrix derived from **G** with dimensions 9 × 305 by 9 × 305 and **S** = a 9 by 9 × 305 summation matrix that sums the contributions of a given TD to the 305-d yield for each trait. The same approach was used to derive $\mathbf{P}_{\text{lact}}$ and $\mathbf{H}_{\text{lact}}$ matrices. Heritabilities for 305-d yields were computed as the ratio of the genetic variances to the sum of the genetic, permanent environmental, herd-year and residual variances. Correlations between traits i and j where computed as the ratio of the covariance cov(i,j) to the square root of the products of the variances of trait i and j.

Residuals were calculated for each DIM as the difference between **y** and $\hat{\mathbf{y}}$, where $\hat{\mathbf{y}}$ = the predicted value obtained by fitting the model. Average residuals can be used to determine the accuracy of the model (Jamrozik and Schaeffer, 1997). Mean values of these residuals over all TD records were estimated and plotted.

Table 1. *Description of test-day data with standard deviation in parentheses*

Item	First lactation	Second lactation	Third lactation
Test-day records used in the analysis	140,187	97,404	62,221
Mean milk yield (kg)	18.2 (6.1)	19.9 (7.0)	20.7 (7.2)
Mean fat yield (kg)	0.59 (0.23)	0.67 (0.27)	0.70 (0.28)
Mean protein yield (kg)	0.56 (0.19)	0.62 (0.22)	0.65 (0.22)
Cows with records used in the analysis	22,538	15,257	9,722
Number of herds	96	93	72
Average number of daughters per bull	13.8	10.4	7.6
Average number of test-day records per cow	7.5	7.3	7.1
Average number of test-day records per herd-test date classes	30.2	22.3	16.4

4.5. Results and Discussion

4.5.1. Lactation Curves

Figure 1 shows the trend of the mean residuals over DIM for milk yield in the first lactation. The residuals were scattered about the horizontal axis. These results indicate a satisfactory description of the lactation curve and an adequate representation of the data by the proposed model. A similar trend of mean residuals over DIM was observed across the lactation trajectory for the second parity. However, the fluctuation around zero was slightly higher in the third lactation which can be explained by fewer TD records in later lactations.

When applying an alternative model (results not shown) with a parametric curve in the fixed part (third-order Legendre polynomials for season-age of calving), and without the random HY effect, undesirably large fluctuations of mean residuals across the lactation were observed, i.e., a large under- or over-estimation of milk yield in the different lactation phases was obtained. Druet *et al.* (2003) also found that the use of fixed classes assured the best fit compared to parametric curves (Legendre polynomials, Ali-Schaeffer curve, and Wilmink curve). Due to their large number of parameters, fixed classes allow more flexibility than do parametric curves. In addition, any record in the parametric curve will influence the whole curve. In contrast, the influence of the data is local in the case of fixed classes. Also, classes of DIM can be cross-classified with other effects with the potential to influence lactation shapes, such as production sectors in our case.

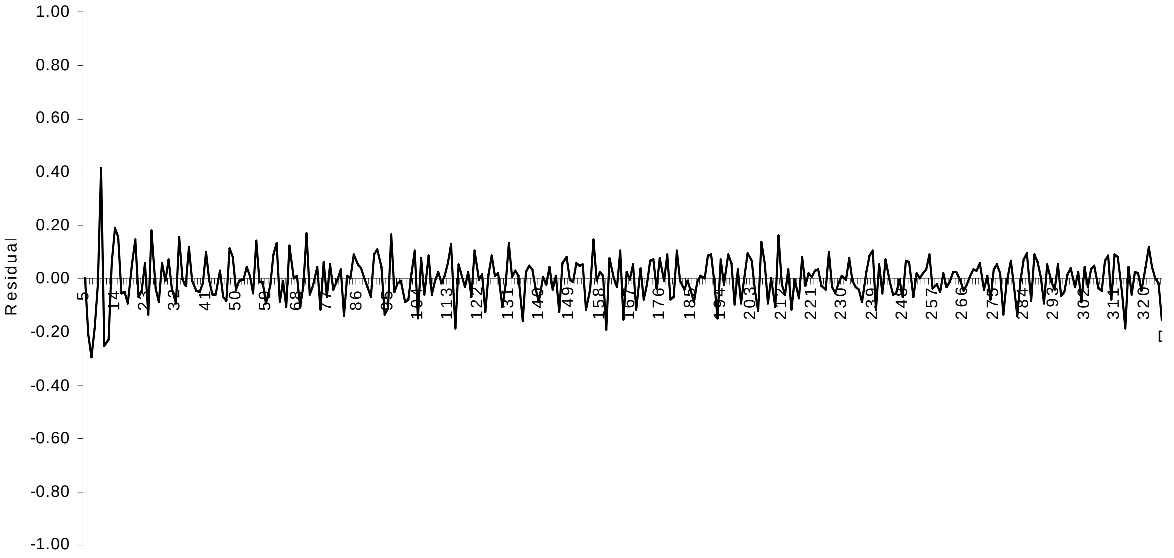

***Figure 1**. Mean residuals (difference between observed and estimated test-day records) by DIM for milk yield in the first lactation.*

4.5.2. Variance Components

Estimates of AG, PE, HY and R variances of the first RR coefficient (intercept) for milk, fat, and protein yields are given in Table 2. All variances increased with parity for all yield traits. Similar trends were reported in previous studies on other data (Rekaya *et al.*, 1999; Zavadilová *et al.*, 2005; Muir *et al.*, 2007). The PE variance was consistently higher than AG, HY and R variances for all traits in the three lactations. Estimated variances increased from the first to the second parity for all traits. However, the differences between all variances in the second and third lactation were small. In general, similar results were found with data from Spanish Holsteins and a repeatability model (Rekaya *et al.*, 1999).

***Table 2**. Posterior means of additive genetic (AG), permanent environmental (PE), herd-year of calving (HY) and residual (R) variances (Posterior SD in brackets) of the first random regression coefficient (intercept) for milk, fat, and protein yields*

	First lactation				Second lactation				Third lactation			
Trait	AG	PE	HY	R	AG	PE	HY	R	AG	PE	HY	R
Milk	1.91 (0.19)	8.46 (0.17)	0.48 (0.08)	2.98 (0.13)	2.71 (0.21)	11.94 (0.26)	0.72 (0.14)	3.58 (0.21)	2.83 (0.32)	12.69 (0.34)	0.71 (0.19)	3.84 (0.30)
Fat (x1000)	1.34 (0.16)	8.47 (0.16)	0.49 (0.09)	16.75 (0.07)	2.06 (0.14)	13.13 (0.26)	0.81 (0.17)	22.5 (0.12)	2.28 (0.45)	13.70 (0.53)	1.01 (0.25)	24.51 (0.18)
Protein (x1000)	1.53 (0.15)	7.83 (0.14)	0.45 (0.08)	4.76 (0.02)	2.07 (0.17)	11.32 (0.22)	0.60 (0.13)	6.31 (0.03)	2.30 (0.33)	11.89 (0.35)	0.73 (0.20)	6.55 (0.04)

Misztal *et al.* (2000) reported that the level and pattern of daily milk yield variances obtained by RR models were heterogeneous. In the present study, the pattern of variance components across the lactation for milk yield is shown in Figure 2. The same patterns were also observed for fat and protein yields. The genetic and PE variances were generally large at the beginning, small in the middle, and moderate at the end of the lactations.

The PE variance estimates were consistently larger than AG estimates throughout the lactation. In general, the trends in the AG and PE variance estimates throughout lactation obtained in this study are comparable to trends found by Olori *et al.* (1999), Druet *et al.* (2005), Strabel *et al.* (2005), and Zavadilová *et al.* (2005). Those authors reported larger estimates of AG and PE variances at the beginning and end than in the middle of the lactation. However, Pool *et al.* (2000) and Druet *et al.* (2003) found opposite trends for AG variance estimates. In those studies, RR models were also applied and Legendre polynomials were used to describe random curves. However, in their analyses, the residual variance was not assumed to be constant during lactation, as in our study. Pool *et al.* (2000) reported that the shape of variance curves across lactation could be modeled with sufficient accuracy by using a third-order polynomial for the genetic part, but a fourth-order Legendre polynomial was needed for the PE. López-Romero and Carabaño (2003) also reported that smaller order of polynomials for AG than for PE could be more suitable. Complexity of environmental effects was increased in our study by including the common HY effect.

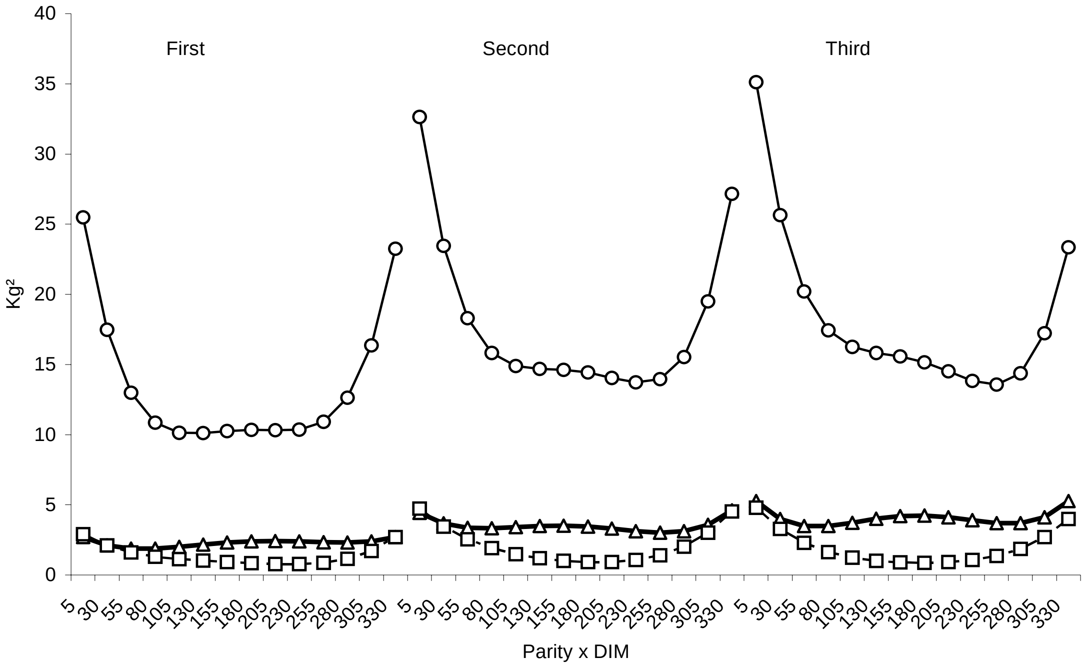

***Figure 2**. Additive genetic (triangles), permanent environmental (circles) and herd-year of calving common environmental variances (squares) of milk yield estimated for the first three lactations of Tunisian Holsteins.*

The HY variances were the smallest compared to the other sources of variance. The HY variances were greatest at the beginning and the end of the lactation and negligible in mid-lactation. For all traits studied, the HY curve variances were typically U-shaped. The same pattern was also reported by Gengler and Wiggans (2001) and de Roos *et al.* (2004) and is in line with the hypothesis that the HY effect catches variance at the beginning and end of the lactations due to specific environmental influences in the different herds, such as calving preparation and dry cow management.4.5.3. Heritability Estimates

Estimates of heritabilities of 305-d yield in the first three lactations are shown in Table 3. Estimates of 305d heritabilities pooled over three lactations and computed from estimated (co)variances were greater than lactation-based estimates and were 0.25, 0.17 and 0.21 for milk, fat and protein yield, respectively. The largest 305-d yield heritalities were obtained for milk yield and the smallest heritabilities were found for fat yield. This finding was also reported by Tijani *et al.* (1999), Lidauer *et al.* (2003), Strabel and Jamrozik (2006), and Muir *et al.* (2007). Reents *et al.* (1995) and Jakobsen *et al.* (2002), however, obtained the smallest heritabilities for protein yield in the first lactation.

Heritabilities for 305-d milk yield in the first three lactations (0.17, 0.18, and 0.18) were similar to the results obtained with a 305-d repeatability model (Ben Gara *et al.*, 2006) on the same population used for this study. They reported a mean average estimate of 0.17 (range: 0.13 to 0.21). The results were also comparable with 0.18, 0.16 and 0.17 obtained by Strabel and Jamrozik (2006) on Polish black and white cattle using large-scale RR models. However, heritabilities of yield traits for the Tunisian Holsteins were smaller than those reported in large Holstein populations (Pool *et al.*, 2000; Jakobsen *et al.*, 2002; de Roos *et al.*, 2004 ; Druet *et al.*, 2005; Muir *et al.*, 2007). de Roos *et al.* (2004) reported large heritability estimates for milk in the first three lactations (0.51, 0.49, and 0.47) using a RR model with nearly the same fixed and random effects as applied in this study. In general, the level and pattern of milk yield heritability obtained with RR models are sensitive to the model applied.

***Table 3**. Posterior means (posterior SD in brackets) of 305-d yield heritabilities for milk, fat, and protein in the Tunisian Holsteins*

Trait	First lactation	Second lactation	Third lactation	Pooled 305-d[1]
Milk	0.17 (0.02)	0.18 (0.01)	0.18 (0.02)	0.25 (0.02)
Fat	0.13 (0.02)	0.12 (0.01)	0.13 (0.03)	0.17 (0.02)
Protein	0.15 (0.02)	0.15 (0.01)	0.15 (0.02)	0.21 (0.02)

[1] *Pooled 305-d yield was defined as the heritability of the average of every trait over three lactations and values were obtained from the summed variances and covariances for the three lactation 305-d yields.*

Misztal *et al.* (2000) and other recent studies have confirmed this fact. Nevertheless, large estimates of AG variances and heritabilities are associated with high milk production levels (de Roos *et al.*, 2004; Gengler *et al.*, 2005; Druet *et al.*, 2005; Muir *et al.*, 2007).

Low AG and heritability estimates have been reported for populations with low to medium production levels (e.g., Carabaño *et al.*, 1989; Strabel and Misztal, 1999; Strabel and Jamrozik, 2006; Gengler *et al.*, 2005; Ben Gara *et al.*, 2006). In Tunisia, state and cooperative herds, most of which have now been dissolved, accounted for almost two-thirds of cows enrolled in the recording system up to 1998. The cooperative and state herd production levels were 5,456 and 6,057 kg milk per cow in 305-d, respectively, over the 10 year period from 1990 to 1999 (Rekik *et al.*, 2003). These lactation means are greater than those reported for Spanish Holsteins (4,982 kg milk in 305-d) in the 1980s (Carabaño *et al.*, 1989). However, they were 1,700 to 2,250 kg less than those recorded in the 1980s on US Holsteins (Carabaño *et al.*, 1989). Heritability estimates for milk and fat yields in the Spanish population ranged from 0.12 to 0.16 and from 0.09 to 0.14 by within and between country analyses with the US data, respectively. Respective estimates obtained in the same study on the US data ranged from 0.27 to 0.37 and from 0.24 to 0.33 for milk and fat yields. In fact, Veerkamp and Goddard (1998) found small heritability estimates of milk, fat, and protein yield (0.13, 0.12, and 0.12, respectively) for cows averaging less than 20 kg of daily milk yield. Our results are, therefore, in line with expectations according to these studies.

Heritabilities of TD milk yields were also determined for selected DIM (Figure 3). The trends for milk and protein TD yield heritabilities showed similar patterns. No undesired extreme estimates at the peripheries of the lactation were found for these two traits in the three lactations studied. Heritabilities were larger in the middle part of lactation than at the beginning or the end. On the other hand, heritability of TD fat yield was high in the beginning of lactation, low at the peak and rose toward the end. In general, a heritability curve characterized by higher values in mid-lactation and lower values at the beginning and end of lactation is more realistic, as it is similar to results from multi-trait models.

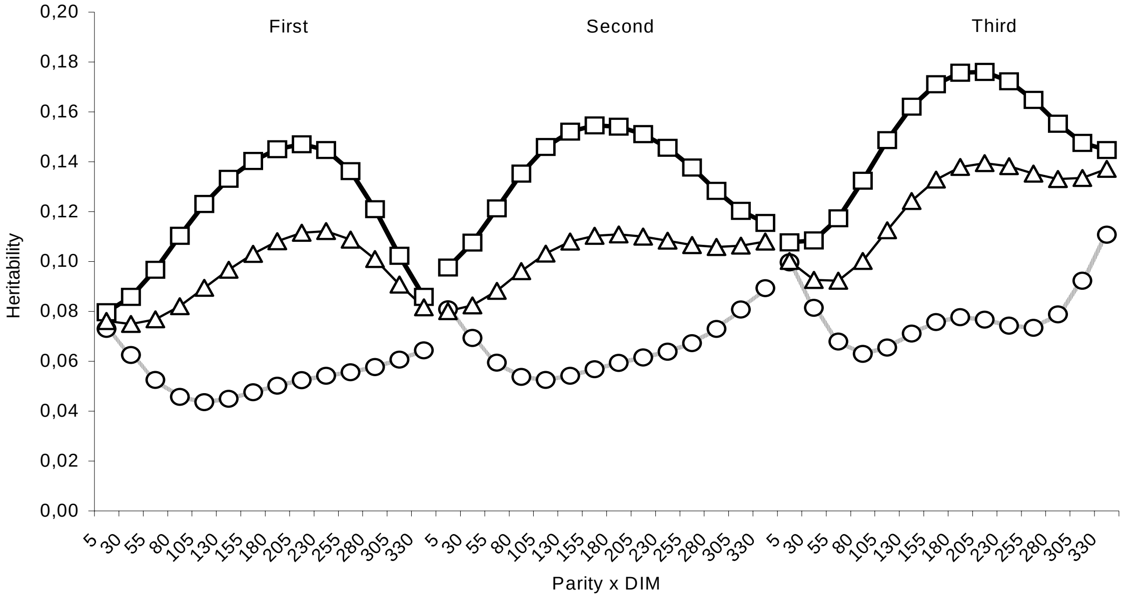

***Figure 3**. Heritability estimates of test-day milk (squares), protein (triangles), and fat (circles) yields.*

The two extremities of lactation are generally more influenced by the farmer decision. Unreasonably large estimates of heritability at the peripheries of lactation have been found in some applications of RR models in which the PE effect was constant along the whole lactation (Jamrozik and Schaeffer, 1997) or when small data sets were analyzed with single-trait models (Misztal and Strabel, 1999). Recently, herd regression curves have been included in the RR model (Gengler and Wiggans, 2001 and de Roos et al., 2004). Reported heritabilities followed the expected pattern with no artifacts observed. The patterns of milk and protein yield heritability curves of our study were in accordance with their findings when compared to a RR model without random HY effect (results not shown). In that model, heritability estimates of TD milk yields were large at the lactation extremities and small in the middle of lactation. In this study, daily heritability estimates of fat were small and did not even exceed 0.06 for two-thirds of the first lactation. The feeding system in Tunisia can be an explanation of the opposite shapes of fat heritability when compared to milk and protein patterns. Most of the farms use high concentrate rations because of moderate quantity and quality of roughages that are readily available. Feeding diets with a high proportion of concentrate and low fiber to dairy cattle can result in decreased pH in the rumen, leading to depression of milk fat percentage (Bargo *et al.*, 2003).

4.5.4. Genetic and Permanent Environmental Correlations

Table 4 shows genetic and PE correlations of 305-d yields. Genetic correlations obtained between the yield traits in first and second lactation (0.64 to 0.86) were the largest among all genetic correlation estimates. Genetic correlations ranged from 0.60 to 0.81 between the second and third lactation and from 0.50 to 0.71 between the first and third lactation. Zavadilová *et al.* (2005) found also that the largest genetic correlations occur between yields in adjacent lactations resulting from a multi-trait RR model.

Genetic correlations (305-d yield) among production traits within lactations were high. They ranged from 0.76 to 0.93 between milk and fat yields, from 0.98 to 0.99 between milk and protein yields, and from 0.79 to 0.96 between fat and protein yields. These estimates were larger than those obtained by Muir *et al.* (2007) using a multiple-trait-multiple-lactation RR TD model in Italian Holsteins. Larger genetic correlation between milk and protein yield than between milk and fat yield was reported also by Jamrozik *et al.* (1998), Tijani *et al.* (1999), and Jakobsen *et al.* (2002). PE correlations (305-d yields) between yield traits within lactations were also high (from 0.97 to 0.99). Largest genetic and PE correlations were found among first lactation yields.

Genetic correlations between milk yields at the same DIM in the first three lactations are given in Figure 4. For all traits, the largest genetic correlations occurred between the first and second lactation, and the lowest were observed between the first and third lactation. The shapes of correlations across DIM showed a similar pattern for all traits and lactations with the lowest estimates at the peripheries of lactation. For milk and protein, the correlations between the same DIM in the consecutive lactations were below 0.7 at the beginning of the lactation, between 0.7 and 0.9 in the middle part and again below 0.7 at the end of lactation. However, for fat yields, the correlations were clearly lower, not exceeding 0.72. They were smaller than 0.5 across the whole trajectory of lactation when estimated between the same DIM of the first and third lactation. Similar shapes of correlation at the same DIM among various lactations were also reported by Strabel and Jamrozik (2006). However, the highest correlations were obtained between the second and third lactation in their analysis.

Table 4. *Genetic (above diagonal) and permanent environmental (below diagonal) correlations (SD in brackets) for 305-d milk, fat, and protein yields*

Trait x Lactation		Milk			Fat			Protein		
		1	2	3	1	2	3	1	2	3
Milk	1		0.86 (0.04)	0.71 (0.05)	0.93 (0.01)	0.66 (0.04)	0.44 (0.08)	0.99 (0.01)	0.85 (0.02)	0.64 (0.06)
	2	0.39 (0.01)		0.81 (0.04)	0.76 (0.04)	0.76 (0.05)	0.58 (0.07)	0.84 (0.03)	0.99 (0.01)	0.77 (0.07)
	3	0.31 (0.02)	0.36 (0.03)		0.64 (0.06)	0.67 (0.08)	0.82 (0.03)	0.69 (0.05)	0.81 (0.05)	0.98 (0.01)
Fat	1	0.98 (0.01)	0.35 (0.01)	0.28 (0.02)		0.64 (0.04)	0.50 (0.09)	0.96 (0.01)	0.78 (0.04)	0.60 (0.07)
	2	0.35 (0.01)	0.98 (0.01)	0.33 (0.02)	0.34 (0.01)		0.60 (0.11)	0.66 (0.04)	0.79 (0.06)	0.66 (0.09)
	3	0.27 (0.02)	0.33 (0.02)	0.98 (0.01)	0.26 (0.02)	0.32 (0.02)		0.45 (0.08)	0.62 (0.07)	0.90 (0.02)
Protein	1	0.99 (0.01)	0.38 (0.01)	0.30 (0.02)	0.98 (0.01)	0.35 (0.01)	0.27 (0.02)		0.84 (0.02)	0.63 (0.06)
	2	0.38 (0.01)	0.99 (0.01)	0.36 (0.02)	0.35 (0.01)	0.99 (0.01)	0.33 (0.02)	0.37 (0.01)		0.78 (0.05)
	3	0.30 (0.02)	0.36 (0.01)	0.99 (0.01)	0.27 (0.02)	0.34 (0.02)	0.99 (0.01)	0.29 (0.02)	0.36 (0.02)	

4.5.5. General Considerations

This study of Tunisian data found several important results. First, results suggested similar heritability values in the second and third lactation. Also their AG variances were more similar when compared to the first parity. However the highest genetic correlation was observed between the first and second lactation. We might speculate that these results indicate that animals in later lactations express their genetic potential differently. Furthermore, Holstein cows in Tunisia originate from temperate regions with more favorable management and climatic conditions than found in Tunisia and may not be well adapted to the environment. This factor may be especially critical in later lactations (i.e. third lactation) when increased production adds another stress factor.

Heritabilties and genetic correlations for fat yields obtained in our study were low compared to most studies using RR models. The most likely explanation is that the high temperature and also the lack of quality forage during parts of the year can lead to decreased productivity, as reported by several authors (Ravagnola *et al.*, 2000; Bouraoui *et al.*, 2002; Bohmanova *et al.*, 2007). As found by Ravagnola *et al.* (2000) fat production seems to decline more strongly than milk or protein yield as a response to heat stress. Ravagnola *et al.* (2000) reported this behavior for fat compared to protein when the temperature-humidity-index exceeds 72 (around 24°C).

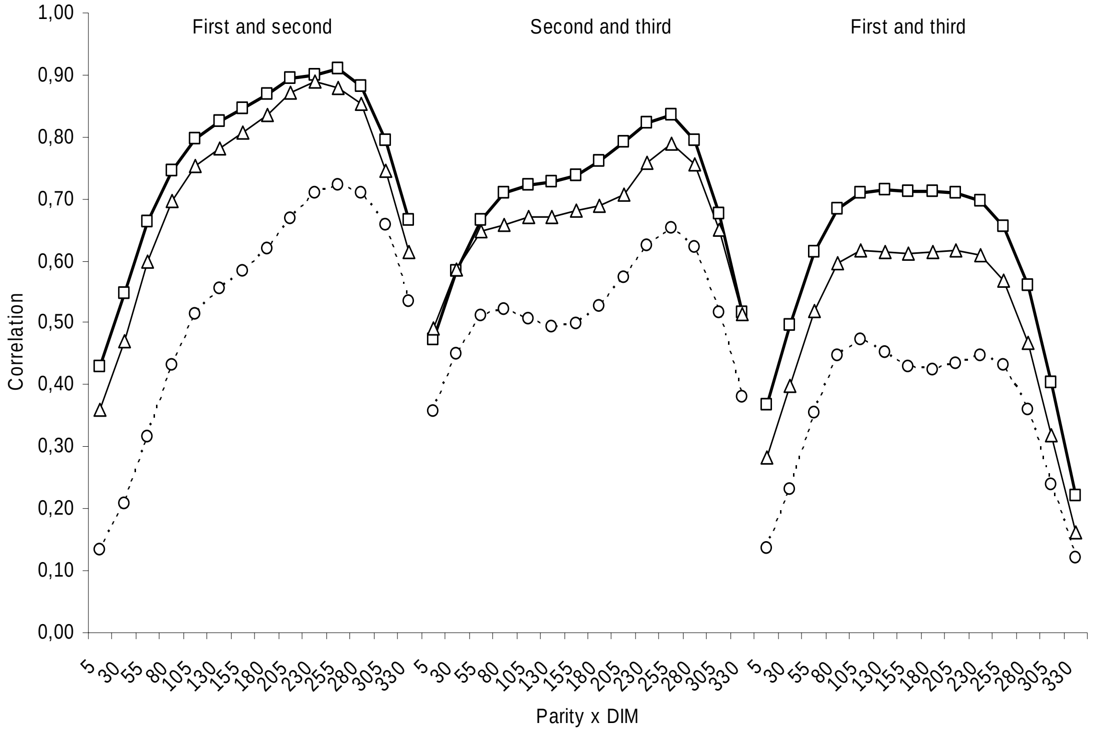

Figure 4. Genetic correlations between the three pairs of lactations at the same DIM for milk (squares), protein (triangles), and fat yields (circles).

The decline for fat was observed over the whole range of temperatures, while for milk and protein; the yields appeared relatively constant until about 24°C and then declined. If the latter value of temperature is considered to cause heat stress, cows in Tunisia are highly affected for almost two-thirds of the year. In addition, the process of the sampling and analysis techniques under harsh climatic situation in Tunisia puts more challenges on the cooling chain from the samples collected to their analysis. One might speculate that this could affect seriously data quality. For routine genetic evaluation it will be important to develop integrated data quality checks similar to those used by Mayeres *et al.* (2003) to detect potentially affected fat content.

4.6. Conclusions

Genetic parameters of milk and protein yields obtained in this study were moderate compared to major reports on Holstein populations, but were low for fat yield. However, parameter estimates were in the same range of previous results obtained in other studies of data from management systems with low to medium production levels. Low heritability estimates are caused by reduced AG and increased PE and R variances. Genetic correlations among production traits within lactations were in general high and ranged from 0.76 to 0.99. On the other hand, the largest correlation coefficient estimates were observed between the first and second lactation yields among all three lactations; while the smallest coefficients were found between the first and third lactations. Selection for increased later lactation yields based on EBV averaged over lactations might therefore be problematic.

Estimates of variance components found in this study may be used for the implementation of a BLUP evaluation for the Tunisian cow population, although the differences in the results for fat yields relative to milk and protein should be further investigated. Data quality management might be still an important issue for this trait. In addition, research on issues not addressed in this study, such as heterogeneity of variances, will eventually be required for implementation of an internationally accepted genetic evaluation system.

4.7. Acknowledgments

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Production performances of Holsteins were negatively affected under the Tunisian conditions. Joint evaluation with their half-paternal sisters in Luxembourg would give more knowlodge about the environmental sensitivity. Estimation of genetic parameters using a multi-country model remains a specific case of within-country parameter estimation and may be available when considering that different traits (countries) are measured on different related animals. Elsewhere, international EBV of sires are estimated by multi-trait sire model using MACE procedure, where records of daughters in different countries are considered as genetically separate traits. This implies that information contributing to the estimation of genetic correlations is coming from common sires with daughters in the different countries. The developed model presented in the previous chapter was therefore used in the next chapter for a first investigation of G × E interaction using Luxembourg and Tunisian Holstein populations by considering milk production traits in each of the two countries as a character state different from the other one and estimating the genetic correlation between them. Most of the links existing among these two populations were built up from the use of semen of common sires proven in different exporting countries. Thus, the objective of the next chapter was to ***study the possibilities of using within- and across-country random regression TD sire models in investigating the magnitude of G x E for milk yield and persistency for Holsteins in Luxembourg (high-input system) and Tunisia (low- to medium-input system)****. The method applied and the results obtained were compiled in a paper accepted for publication in the Journal of Animal Breeding and Genetics.*

Chapter 5

Accessing Genotype by Environment Interaction Using Within- and Across-Country Test-Day Random Regression Sire Models

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H. Hammami, B. Rekik, H. Soyeurt, C. Bastin, E. Bay, J. Stoll, and N. Gengler. 2009.

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5.1. Summary

First-lactation test-day (TD) milk records of Luxembourg and Tunisian Holsteins were analyzed for evidence of genotype by environment interaction (G × E). The joint data included 730,810 TD records of 87,734 cows and 231 common sires. Random regression TD sire models with fourth-order Legendre polynomials were used to estimate genetic parameters via within- and across-country analyses. Daily heritability estimates of milk yield from within-country analysis were between 0.11 and 0.32, and 0.03 and 0.13 in Luxembourg and Tunisia, respectively. Heritability estimates for 305-d milk yield and persistency (defined as the breeding value for milk yield on DIM 208 minus the breeding value on DIM 80) were lower for Tunisian Holsteins compared with the Luxembourg population. Specifically, heritability for 305-d milk yield was 0.16 for within- and 0.11 for across-country analyses for Tunisian Holsteins, and 0.38 for within- and 0.40 for across-country analyses for Luxembourg Holsteins. Heritability for apparent persistency was 0.02 for both within- and across-country analyses for Tunisian Holsteins, and 0.08 for within- and 0.09 for across-country analyses for Luxembourg Holsteins. Genetic correlations between the 2 countries were 0.50 for 305-d milk yield and 0.43 for apparent persistency. Moreover, rank correlations between estimated breeding values of common sires for 305-d milk yield and persistency, estimated separately in each country, were low. Low genetic correlations are evidence for G × E for milk yield production while low rank correlations suggest different rankings of sires in both environments. Results from this study indicate that milk production of daughters of the same sires depends greatly on the production environment and that importing high merit semen for limited input systems might not be an effective strategy to improve milk production.

Keywords: genetic correlation, rank correlation, genotype by environment interaction, random regression.

5.2. Introduction

Biotechnological developments and international trade of frozen semen have led to increased use of AI in cow populations since the 1970s. Nowadays, an AI bull has numerous daughters producing in various production environments. Superior sires are selected on estimated breeding values **(EBV**) from national evaluations. Across countries selection of high merit animals is profitable under the globalization of dairy industries (Banos and Smith, 1991), but breeders' major concern is the choice of appropriate candidates for their production systems. A problem that breeders have to face when choosing semen is that bulls may rank differently for milk yield in country specific environments. Genotype by environment interaction **(G × E)**, differences in trait definitions and national evaluations may all be causes of re-ranking of sires in different production systems (Powell and VanRaden, 2002).

Currently, the multiple-trait across country evaluation procedure used by Interbull permits the estimation of genetic correlations between countries or populations. Then conversion formulas of breeding values from one member to another are derived following each test run. In the international genetic evaluations by the Interbull, G × E is considered and country border delimitation is used as a criterion for environment definition. However, many herds in different countries can be very similar in different production environments. Some more definite descriptions for the environment have been presented (Weigel and Rekaya, 2000; Zwald *et al.*, 2001; Fikse *et al.*, 2003), but still not applied in the routine run.

Evidence of existing G × E inter or intra countries has not been clear in a number of cases. Some studies on field data reported only scaling effects (Boettcher *et al.*, 2003; Fikse *et al.*, 2003; Calus and Veerkamp, 2003; Kearney *et al.*, 2004) while others have reported re-ranking effects (Carabaño *et al.*, 1989; Cienfuegos-Rivas *et al.*, 1999; Ojango and Pollot, 2002). But, nearly all studies have supported the fact that G × E is present when, differences among environmental conditions exist and/or genotypes are diverse (Costa *et al.*, 2000; Ojango and Pollot, 2002; Zwald *et al.*, 2003; Bytyqi *et al.*, 2007). According to Weigel *et al.* (2001), genetic correlations among countries in the northern hemisphere are high. Genetic correlations close to 0.80 have been found among several neighbouring countries in the American continent (Stanton *et al.*, 1991; Cienfuegos-Rivas *et al.*, 1999; Costa *et al.*, 2000; Ceron-Munoz *et al.*, 2004) and among eastern European countries (Rekaya *et al.*, 2001).

The Luxembourg and Tunisian Holstein populations have relied heavily on the continuous importation of semen and heifers from the USA, Canada and some European countries. These two countries have similar medium sized Holstein cow populations. Although Luxembourg and Tunisian populations have distinct management systems, both populations share important ancestors and genetic links between them have strengthened with time (Hammami *et al.*, 2007). Exploitation of G × E would help in designing sustainable breeding programs. Importing countries, especially those with less advanced genetic evaluation programs, need more knowledge about environmental sensitivity in order to adopt the genetic progress achieved in exporting countries and to avoid failure in their breeding program strategies.

The objective of this study was to investigate G × E for milk yield in Holsteins using Luxembourg and Tunisian cow populations by comparing each sire's breeding values from within- and across-country evaluations and by estimating genetic correlation from an across-country model.

5.3. Materials and Methods

5.3.1. Data

Test-day (**TD)** milk records were obtained from primiparous Holstein cows calving in Luxembourg and Tunisia between 1995 and 2006. Luxembourg data were collected by CONVIS Herdbuch, Service Elevage et Génétique, Ettelbruck, Luxembourg and supplied by VIT (Vereinigte Informationssysteme Tierhaltung, Verden, Germany), and included 852,273 records. The Tunisian data contained 306,415 milk yield TD records provided by the Center for Genetic Improvement of the Livestock and Pasture Office. Data sets from the two countries were constructed using only cows with known sires. Herd-year subclasses with less than four records were omitted. Cows were required to have a minimum of five TD records between 5 and 330 DIM. Common sires with at least four daughters in each country were firstly identified. These sires will be called common sires throughout the study. Herds with daughters of common sires were identified in both populations. The data set used for across-country analyses contained all records from these herds, including daughters from common and also from other sires. Descriptive statistics of data sets used for within- and across-country analyses are given in Table 1.

***Table 1**. Descriptive statistics of datasets used for within- and across-country (in brackets) analysis*

Parameter	Luxembourg		Tunisia	
	Mean	SD	Mean	SD
Number of test day records	661,453 (463,534)	-	281,913 (267,276)	-
Number of cows	77,814 (54,121)	-	36,211 (33,613)	-
Number of sires	2,858 (2,436)	-	2,159 (1,914)	-
Number of herds	525 (427)	-	108 (88)	-
Daily milk yield (kg)	21.8 (22.6)	5.8 (5.8)	18.0 (18.2)	6.4 (6.4)
Yield at DIM 80 (kg)	24.2 (25.3)	5.5 (5.3)	20.5 (20.6)	6.5 (6.5)
Yield at DIM 280 (kg)	18.3 (19.0)	5.0 (4.9)	15.0 (15.2)	5.5 (5.5)
Peak yield (kg)	27.5 (27.8)	5.2 (4.8)	23.9 (23.7)	6.5 (6.4)
Days to peak (d)	73.2 (74.4)	21 (23)	65.2 (66.7)	35 (32)
Age at calving (mo)	30.8 (30.4)	3.8 (3.7)	29.2 (29.2)	5.2 (4.3)
TD records / lactation	9.5 (8.5)	1.6 (1.9)	8.2 (7.9)	1.7 (1.9)

The combined pedigree file contained 5,404 individuals and included the Interbull identification, the country of origin and the birth year of each bull. The same information was available for the sire and maternal grandsire of the bull. Among the 4,350 bulls with progeny records, 231 bulls had daughters in both countries. Among the common bulls, there were 80 from the USA, 80 from Germany, 26 from the Netherlands, 18 from Canada, 16 from France and 11 from Italy. Table 2 shows the numbers of daughters and sires by class of daughters per sire common to both country populations.

Table 2 *Number of daughters and sires by class of daughters per sire common to the Luxembourg and Tunisian cow populations*

Class of number of daughters per common sire	Luxembourg		Tunisia	
	Number of sires	Total number of daughters	Number of sires	Total number of daughters
4 – 10	118	887	169	1,013
11-30	39	783	28	522
31-50	18	660	9	325
51-100	15	1,102	9	609
> 100	41	10,989	16	3,889
Total	231	14,421	231	6,358

Age and season at calving were defined differently for each population according to the distribution parameters (mean and SD) of these two factors. Five subclasses for age at calving (< 28, 28 to 30, 31 to 33, 34 to 36 and > 36 mo), and three seasons (January-March, April-August and September-December) were defined for Luxembourg. For Tunisia, six subclasses for age at calving (< 26, 26 to 27, 28 to 29, 30 to 31, 32 to 33 and > 33 mo), and four seasons (September-November, December-February, March-May, and June-August) were defined.

5.3.2. Genetic parameters estimation and evaluation models

Within-country analysis. Data were first analyzed with a random regression (**RR**) TD sire model that was defined within countries. The matrix notation of the model was:

$$\mathbf{y = Xb + Q(Zs + Wp + Hh) + e},$$

where **y** is a vector of TD milk yield of daughters of sires**,** **b** is a vector of fixed effects: herd x test-date; DIM classes for every 25 days nested in age by season of calving; and DIM classes for every 5 days, **s** is a vector of RR coefficients for the sire additive genetic effect (**SA**), **p** is a vector of RR coefficients for cow effect (**CE**) representing permanent environmental effects and the part of the additive genetic effect that can not be attributed to the sire**,** **h** is a vector of RR coefficients of the common environmental effect due to herd-year of calving (**HY**)**,** **e** is a vector of residual effects, **Q** is a matrix of fourth-order Legendre polynomials, and **X**, **Z,** **W**, and **H** are incidence matrices relating observations to the various effects. Residuals were assumed to be constant within DIM intervals.

Across-country analysis. A bivariate RR TD sire model was used to estimate (co)variances for milk yield in both countries. This model combined the within-country models with specific definitions of fixed effects within each country. Milk yield from each country was considered as a different trait. The covariance structure of the bivariate model was:

$$\mathrm{V}\begin{bmatrix}\mathbf{s}\\\mathbf{p}\\\mathbf{h}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{G}&\mathbf{0}&\mathbf{0}&\mathbf{0}\\\mathbf{0}&\mathbf{P}&\mathbf{0}&\mathbf{0}\\\mathbf{0}&\mathbf{0}&\mathbf{H}&\mathbf{0}\\\mathbf{0}&\mathbf{0}&\mathbf{0}&\mathbf{R}\end{bmatrix}$$

where $\mathbf{G}= \mathbf{A} \otimes \mathbf{G_0}$, $\mathbf{P}= \mathbf{I} \otimes \mathbf{P_0}$ and $\mathbf{H}= \mathbf{I}\otimes \mathbf{H_0}$; **A** is the genetic relationship matrix among sires; $\mathbf{G_0}$ is a 10 x 10 (co)variance matrix of the SA regression coefficients. $\mathbf{P_0}$ and $\mathbf{H_0}$ are 10 x 10 block diagonal matrices of CE and HY effects, respectively. All across-country (co)variances in $\mathbf{P}_0$ and $\mathbf{H}_0$ were equal to zero because these effects were considered independent across countries. $\mathbf{R} =\begin{bmatrix}\mathbf{I}\sigma^2{}_l & 0\\ 0 & \mathbf{I}\sigma^2{}_t\end{bmatrix}$, where $\sigma^2{}_l$ and $\sigma^2{}_t$ are the residual variances for milk yield in Luxembourg and Tunisia, respectively.

Genetic parameters. Genetic parameters for milk yield within- and across-country were estimated using the average information restricted maximum likelihood (Misztal *et al.*, 2002). Convergence of the iterative process was declared when the relative differences of consecutive parameters were lower than 10^{-10}. The within-country estimates were used as starting values for the bivariate analysis. SA variance ($\sigma^2_\mathbf{s}$), CE variance ($\sigma^2_\mathbf{p}$), HY variance ($\sigma^2_\mathbf{h}$), and heritability (h^2) at a specific day were computed as: $\sigma^2_\mathbf{s}$ = **qGq'**, $\sigma^2_\mathbf{p}$= **qPq'**, $\sigma^2_\mathbf{h}$ = **qHq'** and $h^2 = \frac{4\sigma^2_\mathbf{s}}{\sigma^2_\mathbf{s}+\sigma^2_\mathbf{p}+\sigma^2_\mathbf{e}}$, where **q** is the vector of the associated Legendre polynomials, **G**, **P** and **H** are the (co)variance matrices for SA, CE and HY random regression coefficients, respectively, and $\sigma^2_\mathbf{e}$ is the residual variance. Genetic parameters for 305-d milk yield were derived using **G**, **P** and **H** (co)variance matrices and 305-d vectors of Legendre polynomials ($\mathbf{q_{305}}$). Vectors of 305-d polynomials were obtained by summing up the five coefficients from day 1 to day 305 for SA, CE and HY effects, respectively (e.g. the SA variance for 305-d milk yield was obtained as: $\boldsymbol{\sigma}^2_{\mathrm{s305}}$ = $\mathbf{q_{305}Gq'_{305}}$). Likewise, the heritability estimate for 305-d milk yield was computed as those for specific DIM but using 305-d variances.

A key issue in genetic evaluation of persistency is trait definition. Gengler (1996) and Swalve and Gengler (1999) reviewed measures of persistency of lactation yields. There were different approaches for the trait definition without clear consensus yet on the best method to model persistency. Nevertheless, a common approach used in several studies is to define persistency as the difference between peak yield and the yield of a test day in late lactation (Jamrozik *et al.*, 1998; Jakobsen *et al.*, 2002; Togashi and Lin, 2004). In this study, persistency was defined as the breeding value for milk yield on DIM 280 minus the breeding value on DIM 80. DIM 80 was chosen because average peak yield occurs at DIM 73 and DIM 65 in Luxembourg and Tunisian Holsteins, respectively. This definition is only an apparent persistency (Gengler, 1996) and does not compare animals for persistency independently of the level of production. In order to obtain real persistency, more functions of mixed-model solutions would be necessary to adjust persistency values for yield. Heritability of apparent persistency was computed as follows:

$$h^2_{pers} = \frac{4 \times \mathbf{q}_{pers}\mathbf{G}\,\mathbf{q}'_{pers}}{\mathbf{q}_{pers}\mathbf{G}\,\mathbf{q}'_{pers} + \mathbf{q}_{pers}\mathbf{P}\,\mathbf{q}'_{pers} + \mathbf{q}_{pers}\mathbf{H}\,\mathbf{q}'_{pers} + 2 \times \sigma^2_{\mathbf{e}}},$$

where $\mathbf{q}_{pers} = \mathbf{q}_{day280} - \mathbf{q}_{day80}$.

Comparison of EBV from within- and across-country analyses. EBV of sires for milk yield were calculated for both within- and across-country models with the BLUPF90iod software (Misztal *et al.*, 2002) using the estimated (co)variance components. As the models used were sire models, EBV were obtained by multiplying SA by 2. Rank correlations between EBV for 305-d milk yield, apparent persistency and RR coefficients were calculated using PROC CORR (SAS, 2002).

5.4. Results

5.4.1. Genetic Parameters

Estimated SA, CE and HY variances for 305-d milk yield by within- and across-country models are given in Table 3. Sire additive variances from the Luxembourg data were larger than corresponding estimates from the Tunisian data, whereas Tunisia had the largest CE variance estimates with both within- and across-country analysis models. The SA variances in the Tunisian population were 49 and 69% smaller than those found for the Luxembourg population for within- and across-country models, respectively. On the other hand, within- and across-country CE variance estimates for the Tunisian population were 19 and 14% larger compared to respective Luxembourg ones. Proportional differences for HY variances were around 45% higher for the Tunisian population by either univariate or bivariate analysis.

Table 3. *Estimates of sire additive genetic (SA), cow (CE) and herd-year common environmental (HY) variances for 305-d milk yield by within and across country analyses*

Variances	Within-country analysis		Across-country analysis	
	Luxembourg	Tunisia	Luxembourg	Tunisia
SE	82,346	41,743	93,712	29,055
CE	743,780	929,460	823,440	963,260
HY	25,878	46,166	27,389	50,284

Eigenvalues and their relative proportions from within- and across-country analyses for the SA, CE, and HY (co)variance matrices are shown in Table 4. The first principal component of the (co)variance matrix among SA regressions obtained from within-country estimates explained more than 90% of the SA variation of milk yield in both countries. Proportions explained by that same component but from the joint analysis were 91 and 86% for Luxembourg and Tunisia, respectively. The first component of the (co)variance matrix among CE regressions was less informative than for the SA effect from both analyses, especially for the Tunisian data. It accounted for 79 and 68% of CE variation in Luxembourg and Tunisia, respectively. The last three principal components of the CE regression from the across-country model explained 9 and 15% of CE variance in Luxembourg and Tunisia but their cumulative relative proportions for SA were only of 2 and 6%, respectively.

***Table 4**. Eigenvalues (Eig) and their relative proportions (Prop) of the total variance for sire additive genetic (SA), cow permanent environmental (CE) and herd-year common environmental (HY) covariance matrices for milk yield in Luxembourg and Tunisia*

Model			Luxembourg					Tunisia				
			1	2	3	4	5	1	2	3	4	5
Within-country	SE	Eig	0.93	0.06	0.02	0.01	0.01	0.47	0.02	0.01	0.01	0.01
		Prop (%)	91.0	6.0	2.0	1.0	0.0	93.0	5.0	2.0	0.0	0.0
	CE	Eig	8.09	1.23	0.53	0.26	0.08	9.98	2.50	1.27	0.69	0.22
		Prop (%)	79.0	12.0	5.0	3.0	1.0	68.0	17.0	9.0	4.0	2.0
	HY	Eig	0.43	0.27	0.08	0.02	0.01	0.74	0.34	0.16	0.02	0.01
		Prop (%)	53.0	34.0	10.0	2.0	1.0	58.0	27.0	13.0	1.0	1.0
Across-country	SE	Eig	1.05	0.08	0.02	0.01	0.01	0.33	0.03	0.02	0.01	0.01
		Prop (%)	91.0	7.0	2.0	0.0	0.0	86.0	8.0	4.0	1.0	1.0
	CE	Eig	8.79	1.34	0.58	0.28	0.09	10.07	2.58	1.30	0.71	0.23
		Prop (%)	79.0	12.0	5.0	3.0	1.0	68.0	17.0	9.0	4.0	2.0
	HY	Eig	0.44	0.28	0.08	0.03	0.01	0.81	0.36	0.17	0.02	0.02
		Prop (%)	52.0	33.0	10.0	4.0	1.0	59.0	26.0	12.0	1.0	1.0

Heritabilities for milk yield at selected DIM, for 305-d milk yield and for apparent persistency, estimated using within- and across-country models, are shown in Table 5. Heritability estimates found for milk yield using the Tunisian data were considerably lower than those obtained using the Luxembourg data. Using the joint data resulted in increased heritability estimates for Luxembourg but partly lowered estimates for Tunisia. Heritability estimates by the within-country model ranged from 0.11 to 0.32 over the lactation length in Luxembourg while Tunisian estimates ranged from 0.03 to 0.13. In joint analyses, these ranges were from 0.12 to 0.34 and from 0.03 to 0.09 for the Luxembourg and Tunisian first lactation curves, respectively. For both countries, heritabilities were higher in the middle than at the beginning or the end of lactation. Heritability estimates for 305-d milk yield and apparent persistency obtained in the Luxembourg population (0.38 and 0.08 by within-country analyses; 0.40 and 0.09 by across-country analyses) were higher than those found for the Tunisian population (0.16 and 0.02 by within-country analyses; 0.11 and 0.02 by across-country analyses).

Genetic correlations between TD milk yields at selected DIM, 305-d milk yields and apparent persistency in Luxembourg and Tunisia are given in Table 5. Genetic correlations between TD milk yields at corresponding DIM were low and ranged from

0.34 to 0.63. Those between 305-d milk yields and persistency were 0.50 and 0.43, respectively.

***Table 5**. Heritability and correlation[1] estimates by within- and across-country analyses for 305-d milk yield, persistency[2], and test-day milk yield at day 5, 30, 80, 155, 280, and 330 of Luxembourg and Tunisian Holsteins*

	Within-country model			Across-country model			
	heritability		r_s[1]	heritability		r_g[2]	r_b[2]
	LUX	TUN		LUX	TUN		
305-d	0.38 (0.02)	0.16 (0.01)	0.34	0.40 (0.02)	0.11 (0.01)	0.50 (0.04)	0.68
Persistency[3]	0.08 (0.01)	0.02 (0.00)	0.26	0.09 (0.01)	0.02 (0.00)	0.43 (0.02)	0.66
5	0.11 (0.01)	0.03 (0.00)	0.08	0.12 (0.01)	0.03 (0.01)	0.40 (0.07)	0.39
30	0.16 (0.01)	0.05 (0.00)	0.19	0.17 (0.01)	0.04 (0.01)	0.34 (0.05)	0.41
80	0.25 (0.01)	0.09 (0.00)	0.32	0.27 (0.01)	0.08 (0.00)	0.38 (0.02)	0.58
155	0.29 (0.01)	0.13 (0.01)	0.35	0.30 (0.01)	0.09 (0.01)	0.52 (0.03)	0.69
280	0.32 (0.02)	0.11 (0.01)	0.37	0.34 (0.02)	0.09 (0.01)	0.63 (0.05)	0.79
330	0.26 (0.04)	0.10 (0.03)	0.35	0.28 (0.06)	0.07 (0.03)	0.50 (0.17)	0.79

[1] *r_s :rank correlation between EBVs of common sires from within-country evaluation*

[2] *r_g :genetic correlation; r_b:rank correlation between EBVs of common sires from across-country evaluation.*

[3] Apparent persistency defined as EBV at DIM 280 – EBV at DIM 80

5.4.2. Estimated Breeding Values of Common Sires

Rank correlations between EBV of common sires for 305-d milk yield, apparent persistency and milk yield at selected DIM estimated by within- (r_s) and across-country (r_b) models are shown in Table 5. Rank correlations from separate evaluations for selected DIM are in the range between 0.08 and 0.37 and are lower than the genetic correlations estimated by the across-country model. Correlations between common sires' EBV for 305-d, apparent persistency and different DIM from across-country evaluation were higher than those obtained from separate evaluations. Rank correlations between EBV of common sires for 305-d milk yield, apparent persistency and RR coefficients estimated separately in Luxembourg and in Tunisia are shown in Table 6. Rank correlations between EBV for 305-d milk yield and EBV for apparent persistency in both countries were 0.16 and 0.25. Low rank correlations were also observed between sires' EBV for the different RR coefficients, 305-d milk yield and apparent persistency. The correlation coefficient between EBV of common sires for the intercept term (a_0) estimated in both countries was similar to that obtained between EBV for 305-d milk yield. But the rank correlation between those common sires' EBV for the linear random regression coefficient (a_1) was slightly different from that between EBV for apparent persistency as defined here. Negative correlations were found between common sires' EBV for either the third (a_2) or the fifth RR coefficient and the rest of the RR coefficients, 305-d milk yield and apparent persistency.

***Table 6**. Rank correlations between estimated breeding values of all common sires[1] for 305-d milk yield, persistency[2] and additive genetic random regression coefficients (a_0, a_1, a_2, a_3, and a_4) in Luxembourg and Tunisia*

		Tunisia						
		305-d	Persistency[2]	a_0	a_1	a_2	a_3	a_4
Luxembourg	305-d	0.34	0.25	0.34	0.33	-0.37	0.27	-0.19
	Persistency[2]	0.16	0.26	0.17	0.28	-0.19	0.02	-0.02
	a_0	0.34	0.25	0.36	0.33	-0.38	0.27	-0.19
	a_1	0.20	0.29	0.21	0.33	-0.25	0.07	-0.05
	a_2	-0.22	-0.34	-0.23	-0.39	0.27	-0.17	0.04
	a_3	0.32	0.21	0.32	0.28	-0.39	0.20	-0.30
	a_4	-0.32	-0.14	-0.33	-0.23	0.39	-0.26	0.32

[1] *Sires with at least 4 daughters in each country.*

[2] *Apparent persistency defined as EBV at DIM 280 – EBV at DIM 80.*

EBV for the linear random regression coefficient (a_1) was slightly different from that between EBV for apparent persistency as defined here. Negative correlations were found between common sires' EBV for either the third (a_2) or the fifth RR coefficient and the rest of the RR coefficients, 305-d milk yield and apparent persistency.

EBV for 305-d milk yield and apparent persistency estimated by within- and across-country models are given in Table 7 for the top 15 sires ranked on 305-d milk yield in Luxembourg. Those top sires with at least 30 daughters in Luxembourg were ranked differently on 305-d milk yield and apparent persistency in both countries. Mean 305-d milk yield EBV of common sires was nearly 5 times higher in Luxembourg than that estimated in Tunisia. EBV for milk yield across lactation for the first 5 of the top 15 sires from separate evaluations are shown in Figure 1. As for total milk yield, it is evident that daughters of these top sires reacted differently to management conditions throughout lactation in both countries. In Luxembourg, the EBV curves of the top 4 sires were flat after peak yield. This trend was observed for only the top 3 sires in Tunisia. The sire s5 had similar curves of EBV for milk yield in Luxembourg and in Tunisia. However, the sire s4 showed a curve in Tunisia opposite to that observed in Luxembourg. EBV curves of those same sires from across-country evaluation were comparable to within- country EBV curves (Figure 2).

***Table 7**. Breeding values for 305-d milk yield and apparent persistency[1] of lactation for sires with more than 30 daughters in Luxembourg and in Tunisia from within- and across-country evaluations*

	Within-country analysis						Across-country analysis			
	Luxembourg			Tunisia			Luxembourg		Tunisia	
Sires	Daughters (n)	Milk[2] yield	Apers[1]	Daughters (n)	Milk[2] yield	Apers[1]	Milk[2] yield	Apers[1]	Milk[2] yield	Apers[1]
S1	31	1188	0.38	169	257	0.27	1149	0.47	229	0.37
S2	113	1173	0.36	124	141	0.33	1117	0.43	111	0.50
S3	35	1123	-0.01	33	133	-0.08	1006	0.09	206	0.17
S4	33	883	-0.50	56	-215	0.48	688	-0.59	-60	0.51
S5	32	695	-0.74	410	239	-0.34	678	-0.63	259	-0.30
S6	903	649	0.29	33	126	0.55	663	0.54	90	0.63
S7	132	644	-0.12	32	91	0.21	597	-0.10	121	0.24
S8	235	598	-1.39	100	26	-0.20	567	-1.29	42	-0.35
S9	660	592	-0.13	29	-179	0.02	544	-0.10	-2	0.26
S10	227	504	-0.29	26	-116	-0.03	469	-0.20	12	0.06
S11	512	479	-0.02	44	-42	0.26	434	-0.01	102	0.22
S12	91	395	0.07	93	342	-0.01	392	0.25	226	0.19
S13	297	382	0.00	20	-23	0.12	351	0.04	54	0.23
S14	71	347	-0.77	35	-4	-0.34	326	-0.65	16	-0.26
S15	227	330	-0.21	52	-97	-0.26	303	-0.14	-6	-0.11
Mean[3]	63	510	-0.16	29	107	0.02	479	-0.06	105	0.11
SD[3]	127	273	0.39	81	134	0.18	235	0.34	103	0.19

[1] *Apparent persistency defined as EBV at DIM 280 – EBV at DIM 80.*

[2] *EBV for 305-d milk yield (kg).*

[3] *Mean and standard deviations (SD) for all common sires with at least 4 daughters in each country (231 sires).*

5.5. Discussion

The present study combined data from two Holstein populations where breeding programs rely on germplasm importation. The Tunisian environment can be described as a low- to medium- input system under North African conditions, whereas the Luxembourg one can be viewed as a high-input system in Western Europe. Genetic correlations from the across-country model and rank correlations between common sires' EBV estimated by separate and joint evaluations were used to assess the magnitude of G × E using a RR sire model. The RR sire model used in this study is justified by the fact that the Luxembourg and Tunisian Holstein populations have genetic links from using common sires. Sigurdsson *et al.* (1996) reported that genetic parameter estimates are highly dependent on the genetic ties between the populations. However, sire models ignore relationships among cows and assume that mating is random, which may result in an underestimation of genetic parameters when mating partners of imported sires are not considered. The bias in the genetic parameter estimates using sire models should be minimized given that semen is purchased in Luxembourg and Tunisia from various origins without restrictions as to the specific countries of purchase or the limitation on price, and no preferential mating is operating, especially in Tunisia where imported semen is generally randomly distributed across herds.

The SA, CE and HY random effects were modelled with fourth-order Legendre polynomials to provide equal opportunity of variation for all components. However, Table 4 shows that eigenvalues of the SA (co)variance matrix for the last two components were small and the cumulative proportion of variation explained by the first three components was large (> 98%) for both populations. Nevertheless, four components were needed to account for 98% of variation in the case of the CE effect. This may imply that the number of parameters may be reduced and the sire effect could be sufficiently modelled with only third order Legendre polynomials. On the other hand, fourth order Legendre polynomials seemed to be a good fit for the CE and HY effects even though the number of estimated parameters increased. Calus and Veerkamp (2003) assessed environmental sensitivity of genetic merit for production traits using 14 environmental parameters in a random regression model. These authors found that the most highly estimable and significant effects of G × E could be sufficiently detected using only second order Legendre polynomials for almost all environmental parameters studied.

Variance component estimates from the within-country model for 305-d milk yield were different in the two populations (Table 3). Sire additive effect variances were low and CE variances were large in Tunisia compared to Luxembourg estimates. CE estimates using sire models are generally high because they include three-quarters of the additive genetic variance. Jamrozik *et al.* (2002a) also reported specific differences in the absolute value and correlations between RR coefficients among four different Holstein populations using a RR TD animal model. There were differences in variance components between Canada and Italy (intensive management systems) and Australia and New Zealand (rotational grazing systems). In this study, the large CE variances found in Tunisia may be caused by limited management, constrained feeding resources and stressful climatic conditions. Reduced SA variances in Tunisia could be mainly explained by the difficulties encountered by high producing daughters in expressing their genetic potential under the Tunisian production environments where the within-herd correlations of genotype x management (essentially the feeding system) are small due to scarcity of quality forages when compared to versatile feeding resources in Luxembourg.

Heritabilities of daily and 305-d milk yields in Luxembourg were moderate and comparable to estimates found in other studies using RR TD animal models (Tijani *et al.*, 1999; Jakobsen *et al.*, 2002; Muir *et al.*, 2007). Similar low heritabilities of milk production traits as obtained in this study for Tunisia have also been found in low-input systems (Carabaño *et al.*, 1989; Castillo-Juarez *et al.*, 2000; Raffrenato *et al.*, 2003; Hammami *et al.*, 2008). Wiggans and Van Vleck (1978) reported that genetic expression of differences among sires will be greater when environmental conditions favour phenotypic expression of milking potential. Selection practices in Tunisia and Luxembourg may also be reasons for differences in genetic parameters between the populations. The main breeding objective in Tunisia is milk yield while breeders in Luxembourg choose on a composite index that includes durability, health and reproduction traits in addition to milk yield (Miglior *et al.*, 2005). Selection based on progeny testing or a combined index could possibly lead to somewhat greater genetic response. Furthermore, although national milk recording schemes in both countries are organized in accordance with international standards, animals' identifications between AI centres, milk recording organizations and farmers and herd book registration are available and better structured in Luxembourg compared to those in Tunisia. Apparent persistency (not adjusted for milk production level) was defined here as the difference between DIM 80 and DIM 280. The pregnancy effects were ignored because of the lack of records on reproduction in the data. The low heritability estimates of this trait as defined here for both populations should be considered cautiously.

The genetic correlation for 305-d milk yield between Luxembourg and Tunisia was low (0.50) compared to estimates higher than 0.80 reported by most of across-country studies on Holsteins (Carabaño *et al.*, 1989; Stanton *et al.*, 1991; Costa *et al.*, 2000; Rekaya *et al.*, 2001; Weigel *et al.*, 2001). However, our result is comparable to that found by Ojango and Pollot (2002) for 305-d milk yield (0.49) between the Kenyan and British populations. Cienfuegos-Rivas *et al.* (1999) reported a genetic correlation of 0.63 between the USA and Mexico and Jamrozik *et al.* (2002a) found a slightly higher correlation (0.66) between Italy and New Zealand using a multiple-country RR TD animal model. In a study on G × E between New Zealand and Canada, Charagu and Peterson (1998) obtained a low genetic correlation (0.29) between both countries and reported significant G × E for first lactation protein yield. These authors attributed the significant interactions to the large differences of protein yield among New Zealand cows compared to the small differences among their Canadian paternal half-sisters. Many studies assessing the suitability of directly using national EBV in the USA to select sires for use in the Latin American countries (Stanton *et al.*, 1991; Costa *et al.*, 2000; Cienfuegos-Rivas *et al.*, 1999) found lower heritability estimates for milk traits in Latin American countries than in the USA, indicating a lower genetic expression of superior genes under tropical conditions than where they were selected. Genetic correlations found in these studies were significantly different from one. The same studies concluded that the significant change in the ranking of sires based on their EBV was a good indicator of G × E between the production environments. Low genetic correlations found in this study may indicate that superior sires identified under Luxembourg production conditions may not perform as well in the Tunisian environments.

Most of the across-country data were analysed using total lactation yields (lactation models) rather than TD records. In addition, those studies were based on data collected on populations that have undergone selection, whereas the current study was based on TD yields recorded on the populations with no proper progeny testing programs. TD records are more informative for assessing G × E than the total lactation records. Indeed, using TD records allow for increased information per sire across the whole lactation length. The use of a herd-TD sire model is more opportune when a large number of observations (TD records) per sire are collected in a wide range of environments compared to the use of lactation records (Hayes *et al.*, 2003). Genetic correlations for milk yield between Luxembourg and Tunisia obtained early in lactation were low compared to those found for late lactation and 305-d milk yield (Table 5). We can speculate that feeding level (in quantity and quality) and management care, necessary for this crucial phase of lactation, were not satisfactory under the Tunisian environments. Thus, the genetic ability to convert rough forages and high grain diet into milk in Luxembourg could be identified as a trait different from the genetic ability to convert poor quality forages and by-products into milk in Tunisia, where breeders other than those in the north of the country purchase conserved roughages and concentrate from the market to feed cows. The low genetic correlations found in this study indicated potential interactions between daughters' performances in Luxembourg and Tunisian environments and could result in considerable re-ranking of sires for daily and 305-d milk yields and apparent persistency.

In this study, correlations of common sires' EBV for 305-d milk yield and apparent persistency from within-country evaluations were smaller than corresponding genetic correlations, whereas rank correlations from the across-country analysis were higher than those obtained from the within-country analysis (Table 5). These results are in concordance with those reported from single- and multiple-country analyses of data recorded on four large Holstein populations using TD animal models (Jamrozik *et al.*, 2002a; Jamrozik *et al.*, 2002b). Jamrozik *et al.* (2002a) found that the lowest genetic correlation (0.66) for total milk yield was obtained between Canada and New Zealand, while the highest correlation (0.83) was obtained between Australia and New Zealand. Jamrozik *et al.* (2002b) found that correlations between common sires' EBV from single-country models were smaller than corresponding genetic correlations and ranged from 0.64 (Canada-New Zealand) to 0.75 (Canada-Italy), whereas those from multiple-country evaluations were higher and ranged from 0.93 (Canada-New Zealand and Italy-New Zealand) to 0.96 (Canada-Italy, Australia-Canada, Australia-Italy and Australia-New Zealand). In spite of these high correlations, Jamrozik *et al.* (2002b) concluded that there was re-ranking of sires on different country scales. Correlations between EBV of common sires for 305-d milk yield, apparent persistency and RR coefficients from within-country analyses were low (Table 6). Low correlations for 305-d milk yield and apparent persistency obtained between Luxembourg and Tunisia indicated re-ranking of sires in both countries. In fact, re-ranking of sires on milk yield and apparent persistency was observed for top common sires using either within- or across-country models (Table 7). Moreover, differences between Luxembourg and Tunisia in the mean and standard deviation of common sires' EBV were large in a pattern similar to that observed for phenotypic and genetic variances. Estimates of rank correlations between EBV of common sires at selected DIM were low, especially at the beginning of lactation. Thus, re-ranking of common sires between both countries was more important across the lactation curve compared to re-ranking of sires on 305-d milk yield. Moreover, curves of EBV for milk yield of the top 5 sires from within-country evaluations (Figure 1) and those from the across-country evaluations (Figure 2) may translate differences in genetic expressions for milk production of daughters of those sires throughout lactations between both environments. However, there were only 15 bulls with at least 30 daughters in both countries. Furthermore, different average test-day records between both populations in addition to low genetic parameter estimates, especially from the Tunisian data, may have contributed to observed differences in EBV curves.

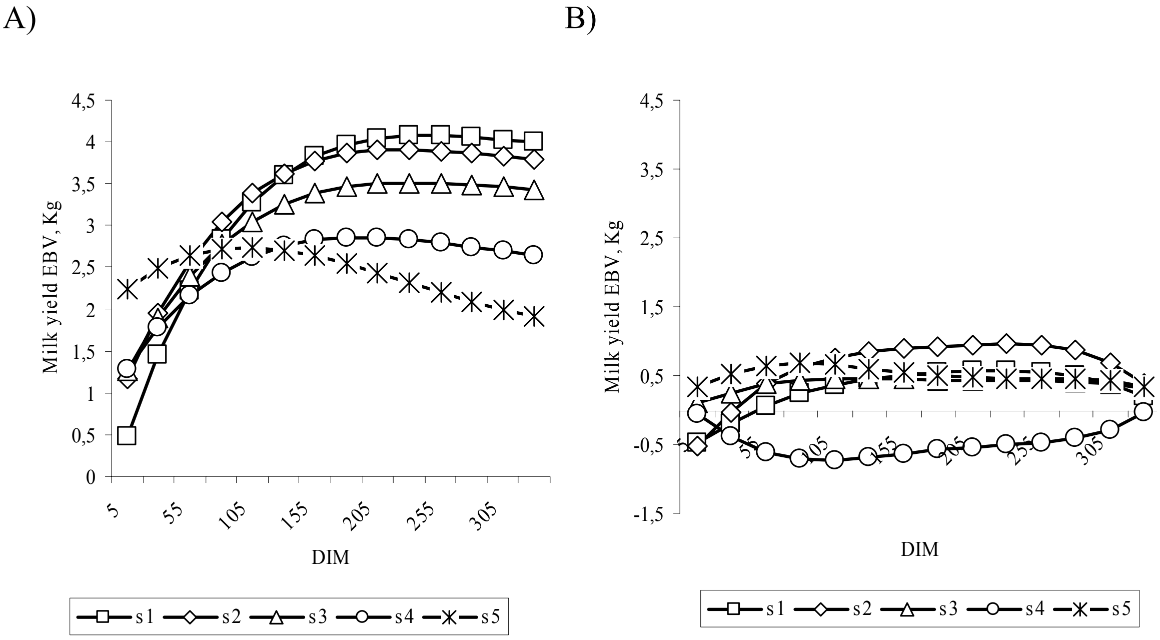

Figure 1. *Estimated breeding values of the five top ranked sires for 305-d milk yield across lactation in A) Luxembourg and in B) Tunisia.*

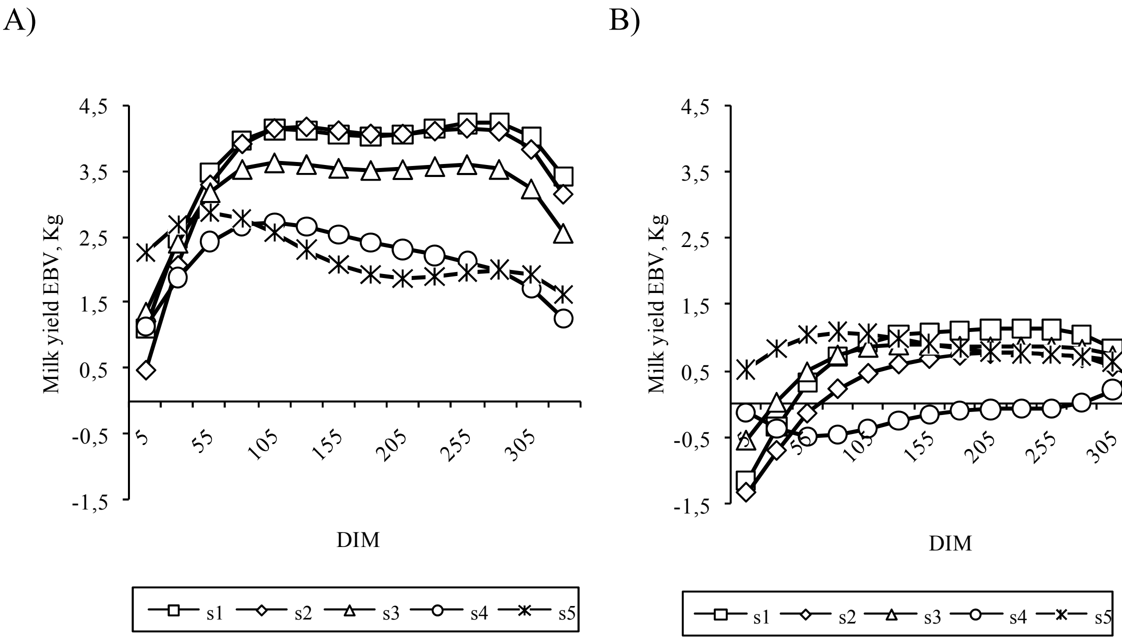

Figure 2**.** *Estimated breeding values of the five top ranked sires for 305-d milk yield across lactation in A) Luxembourg and in B) Tunisia from across-country analysis.*

5.6. Conclusions

Heritabilities of daily and 305-d milk yields and persistency were low under the Tunisian conditions compared to those obtained under the Luxembourg production environment. Low genetic parameters obtained for the Tunisian Holsteins result from reduced SA variances and increased CE variances. In contrast to daughters of sires in Luxembourg, stressful climatic conditions, constrained feeding resources and limited management may all have contributed to impeding daughters of superior imported sires from expressing their genetic potentials in Tunisia. The magnitude of G × E for milk yield between Luxembourg and Tunisia is important and was comparable to G × E found between pairs of countries with diverse production systems and divergent climatic conditions. Breeding programs in Luxembourg and in Tunisia depend on semen imports from different origins. Interactions between imported genes and local environments should be taken into account when choosing semen. In Tunisia, reduced genetic expression indicates that changing and/or improving breeding schemes is justified. The question remains how this can be achieved in the current situation. Tunisia, where production environments are considered as low- to medium-input systems, should purchase well-adapted imported semen and should implement in the near future a local progeny testing scheme. Depending on the possibilities to restrict environmental stressor effects (feeding, management and health care), cross-breeding could be opted for by using local and exotic breeds or crossing different exotic breeds that are adapted to the local production environment.

5.7. Aknowledgments

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The main objective of the previous study was to apply an across-country random regression TD sire model for genetic parameters estimation and evaluation, and to compare across-country EBV with those obtained by the within-country models. The approach used had the same limitations as the international genetic evaluation of bulls under MACE where all genetic links where based on the sires of the cows in production. As previously reported in Chapter 3, Tunisia imported many heifers from Germany and the Netherlands, from which almost half of the Luxembourg ancestors originate. Also maternal grand-sires of cows in both countries are related. For these facts ignoring the additive relationships among cows in Luxembourg and Tunisia could be a source of bias in genetic parameters estimation via a sire model. Being aware of these issues the sire model was extended to an animal model. So, the G × E interaction was assessed for the first lactation milk yield using Luxembourg and Tunisian field data in a random regression TD animal model. Results compiled in an original article published in Journal of Dairy Science are presented in Chapter 6. The main objective of this paper was to ***investigate the magnitude of G x E for milk yield and persistency based on a random regression TD animal models using the country border delimitation as environmental character state****.*

Chapter 6

Genotype x Environment Interaction for Milk Yield in Holsteins Using Luxembourg and Tunisian Populations

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6.1. Interpretive Summary

Luxembourg and Tunisia have relied upon semen and heifer imports to improve the milk production. First lactation milk yields of daughters of common sires were used to estimate genetic parameters of milk production throughout lactation and to rank sires on their EBV in these 2 distinct environments. Genetic variances were large and permanent environmental variances were small under Luxembourg management circumstances, relative to the Tunisian data. Furthermore, ranking of sires differed between the 2 populations. Results suggest that Holsteins ranked high on milk yield in good environments would not necessarily perform as well in less favorable management conditions.

6.2. Abstract

Test day (**TD**) milk yield records of first lactation Holstein cows in Luxembourg and Tunisia were analyzed using within- and between-country random regression TD models. Edited data used for within-country analysis included 661,453 and 281,913 TD records in Luxembourg and Tunisia, respectively. The joint data included 730,810 TD records of 87,734 cows and 231 common sires. Both data sets covered calving years 1995 to 2006. Fourth order Legendre polynomials for random effects and a Gibbs sampling method were used to estimate variance components of lactation curve parameters in separate and joint analyses. Genetic variances of the first 3 coefficients from Luxembourg data were 46 to 69% larger than corresponding estimates from the Tunisian data. Inversely, the Tunisian permanent environment variances for the same coefficients were 52 to 65% larger than the Luxembourg ones. Posterior mean heritabilities of 305-d milk yield and persistency, defined as estimated breeding values (**EBV**) at DIM 280 – EBV at DIM 80, from between country analysis were 0.42 and 0.12, and 0.19 and 0.08 in Luxembourg and Tunisia, respectively. Heritability estimates for the same traits from within-country analyses, mainly from the Tunisian data, were lower than those from the joint analysis. Genetic correlations for 305-d milk yield and persistency between countries were 0.60 and 0.36. Product moment and rank correlations between EBV of common sires for 305-d milk yield and persistency from within-country analyses were 0.38 and 0.41 and 0.27 and 0.26, respectively. Differences between genetic variances found in both countries reflect different milk production levels. Moreover, low genetic and rank correlations suggest different ranking of sires in the 2 environments, which implies the existence of G×E for milk yield in Holsteins.

Keywords: Milk yield, genetic parameters, genotype by environment interaction, Holsteins

6.3. Introduction

Several countries with developing dairy industries have opted for the importation of semen and heifers to replace indigenous breeds. The high yielding Holstein is the most popular among all dairy breeds worldwide. This strategy would be effective if imported animals performed as well in less favorable management circumstances as they would in the environments in which they were selected. Banos and Smith (1991) reported that unfavorable genotype-by-environment interaction (**G×E**) would reduce potential benefits from a strategy based on the importation of superior germplasm. Payne and Hodges (1997) also reported that ignoring G×E when production environments in exporting and importing countries vary widely can lead to expensive failures.

G×E occurs when the performance of different genotypes is not identically affected by different environments. The definition of environment should not include only physical and climatic conditions, but also production and health management, economic constraints, and prevailing agricultural policies (Stanton *et al.*, 1991). Studies on G×E vary from controlled experiments with a few hundred animals (Veerkamp *et al.*, 1995; Beerda *et al.*, 2007) to modeling large field data sets (Weigel *et al.*, 2001; Zwald *et al.*, 2003). Only scaling effects caused by heterogeneous genetic variances were reported by almost all within-country analyses of milk yield in Holsteins (Calus *et al.*, 2002; Raffrenato *et al.*, 2003; Fahey *et al.*, 2007). Furthermore, high genetic correlations were found between countries from the same ecological zone (Weigel *et al.*, 2001) with no evidence of G×E. On the other hand, studies on G×E between countries with different climatic conditions and production systems (Stanton *et al.*, 1991; Costa *et al.*, 2000; Ojango and Pollot, 2002) were rare. In these studies, genetic correlations between countries suggest the existence of G×E for milk yield in Holsteins. Moreover, Stanton *et al.* (1991) and Costa *et al.* (2000) found that the response to selection was smaller in low-input systems than in high-input ones.

Milk yield has been the main breeding objective in Tunisia, whereas a composite index that includes durability, health, and reproduction traits in addition to milk yield is the selection criterion currently used in Luxembourg (Miglior *et al.*, 2005). The Luxembourg Holstein population originally included one-third non-Holstein Red and White dairy cows. Breeders in Luxembourg imported heifers mainly from Germany. Tunisia started importing purebred pregnant Friesian heifers from the Netherlands in 1970. Holstein semen and heifers were then imported from Canada, the United States, and some European countries (Hammami *et al.*, 2007). As in Tunisia, breeders in Luxembourg are currently using semen from mostly North-American and European Holstein sires. Therefore, average additive genetic relationships and genetic similarity between the Luxembourg and Tunisian cow populations have increased with time as a result of continuously using common sires proven in foreign high-input environments (Hammami *et al.*, 2007). The Tunisian environment can be described as a low- to medium-input system, whereas the Luxembourg one as a high-input system. Quantifying interactions between imported germplasm and Luxembourg and Tunisian environments is important for both populations to evaluate and adjust their breeding strategies if necessary. The objective of this study was to assess G×E for first lactation milk yield in Holsteins using Luxembourg and Tunisian field data.

6.4. Materials and Methods

6.4.1. Data

First lactation test day (**TD**) records were available for Luxembourg and Tunisian Holstein cows from 1995 to 2006. Luxembourg data were provided by United Datasystems for Animal Production [Vereinigte Informationssyteme Tierhaltung (VIT), Verden, Germany]. Data were collected from herds under official milk recording by CONVIS Herdbuch, Service Elevage et Génétique, Ettelbruck, Luxembourg. This data set included 852,273 TD records. Tunisian data were obtained from the official milk recording maintained by the Center for Genetic Improvement of the Livestock and Pasture Office (OEP) and included 306,415 TD records. Retained records from the Luxembourg and Tunisian data sets were those of cows with known sires and having at least 5 TD records between 5 and 330 DIM. Records from herds with less than 4 years of performance data were omitted. Furthermore, only herd-year subclasses with at least 4 cow records were kept. After editing, the remaining data for both the Luxembourg and Tunisian cow populations included 943,366 TD records of 114,025 cows. Data structures and descriptive characteristics are given in Table 1.

A combined pedigree file was also created from the Luxembourg and Tunisian source files and by cross-checking with international pedigree files (Hammami *et al.*, 2007). This file included genealogical records on 166,980 animals born between 1927 and 2004. Total numbers of sires with progeny records were 2,546 and 2,035 in Luxembourg and Tunisia, respectively. In order to create a dataset that maximized links without destroying initial data structure the following strategy was used. First we selected common sires with at least 4 daughters in each country. These sires are called common sires throughout the study. Herds with daughters of common sires were identified in both populations. Data used in the joint analysis contained all records from these herds, on daughters from common and other sires. The final joint data included 730,810 TD records of 87,734 cows.

Age at calving and the calving season were defined to account for specificities of each population. Four seasons (September-November, December-February, March-May, and June-August) for Tunisia and 3 seasons (January-March, April-August, September-December) for Luxembourg were identified. And age at calving was classified into 5 classes (< 28 mo, 28 to 30, 31 to 33, 34 to 36, and > 36 mo) for the Luxembourg population and 6 classes (< 26 mo, 26 to 27, 28 to 29, 30 to 31, 32 to 33, and > 33 mo) for the Tunisian population, respectively. Different age at calving classes were used to account for dissimilar ranges of calving age in the 2 countries (Table 1).

***Table 1**. Production descriptors[1,2] with SD in brackets and some environmental characteristics[3] for the Luxembourg and Tunisian Holstein populations*

Parameter		Luxembourg	Tunisia
Number of test day records[1]		661,453	281,913
Daily milk yield[1] (kg)		21.8 (5.8)	18.0 (6.4)
Peak yield[1] (kg)		27.5 (5.2)	23.9 (6.5)
Days to peak[1] (day)		73.2 (21)	65.2 (35)
Age at calving[1] (mo)		30.8 (3.8)	29.2 (5.2)
TD records / lactation[1]		9.5 (1.6)	8.2 (1.7)
TD records per herd test-date class[1]		9.4 (6.1)	36.1 (37.4)
Percentage of calving[1] from :	September to November	35.4	21.3
	December to February	25.0	29.6
	March to May	12.9	26.2
	June to August	26.7	22.9
Number of lactations[2] in 2004		13,371	12,739
Total milk yield per recorded cow for all completed lactations[2] (kg) in 2004		7,946	6,220
Calving interval[2] (day) in 2004		401	444
Average herd size[2] in 2004		46.2	110.0
Average maximum temperature in summer[3] (°C)		22.0	32.7
Average maximum temperature in winter[3] (°C)		4.2	16.7
Annual precipitation[3] (mm)		760	422

[1] *First lactation parameters from the within-country datasets.*
[2] *Figures from ICAR (2007) based on national performance recording statistics.*
[3] *Figures from www.freemeteo.com (2007).*

6.4.2. Analysis

Genetic parameters and evaluations were obtained from single and joint analyses of Luxembourg and Tunisian data by a random regression TD animal model. In matrix notation, the within-country model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}\,(\mathbf{Za} + \mathbf{Zp} + \mathbf{Wh}) + \mathbf{e},$$

where **y** is a vector of TD milk yields**, b** is a vector of the fixed effects: herd × test-date, age × season of calving × classes of 25 DIM, and classes of 5 DIM, **a** is a vector of random regression coefficients for animal genetic (**AG**) effect**, p** is a vector of random regression coefficients for permanent environmental (**PE**) effect**, h** is a vector of random regression coefficients for herd-year of calving common environmental effect (**HY**)**, e** is a vector of residual effects, **Q** is a matrix of Legendre polynomials, and **X**, **Z,** and **W** are incidence matrices relating observations to various effects. Residuals were assumed to be constant within DIM intervals. Legendre polynomials were of order 4 with: $q_{t0} = 1$, $q_{t1} = \sqrt{3}\,x$, $q_{t2} = \sqrt{5}\,(1.5x^2 - 0.5)$, $q_{t3} = \sqrt{7}\,(2.5x^3 - 1.5x)$ and $q_{t4} = \sqrt{9}\,(35x^4 - 30x^2 + 3)/8$, where $x = -1 + (t - 1)/(330 - 1)$ and t is DIM. Higher order polynomials were used in this study than by Hammami *et al.* (2008) because extreme values for the genetic variance at the beginning and end of lactation were found in that study. Higher order regressions allowed testing the hypothesis that they better modelled variance curves across lactation (Pool *et al.*, 2000). An equal order of fit for AG, PE, and HY was used in order to provide equal opportunity of variation for all components.

The same model from above was used for the joint analysis, but extended to a bivariate model; records from Luxembourg and Tunisia being considered 2 distinct, correlated traits. Definitions of fixed and random effects remained the same but were trait specific and nested within country.

Expectations and covariance structure for random effects were defined as follows:

$$E(\mathbf{y}) = \mathbf{Xb},\ E(\mathbf{a}) = 0,\ E(\mathbf{p}) = 0,\ E(\mathbf{h}) = 0,\ E(\mathbf{e}) = 0,$$

and

$$V(\mathbf{a}) = \mathbf{G},\ V(\mathbf{p}) = \mathbf{P},\ V(\mathbf{h}) = \mathbf{H},\ V(\mathbf{e}) = \mathbf{E},$$

where $\mathbf{G = A \otimes G_0, P = I \otimes P_0, H = I \otimes H_0}$; $\mathbf{A}$ is the additive genetic relationship matrix; $\mathbf{G_0}$, $\mathbf{P_0}$, and $\mathbf{H_0}$ are 10 × 10 covariance matrices for AG, PE, and HY regression coefficients, respectively; All between-country covariances in $\mathbf{P_0}$ and $\mathbf{H_0}$ were equal to zero because no herd spans across countries and we assumed no cow moved between Tunisia and Luxembourg during her first lactation. The matrix $\mathbf{E}$ was considered to be diagonal, representing residual variances for milk yield in Luxembourg and Tunisia.

Genetic parameters from both single and two country models were estimated with a Bayesian approach via a Gibbs sampling algorithm (Misztal *et al.*, 2002). Single chains of 120,000 samples (with 20,000 discarded) were generated for separate analyses on each country's data. For the joint analysis, a chain of 160,000 samples (with 30,000 as burn-in period) was generated. Convergence of Gibbs chains was monitored by inspecting plots of selected realizations.

Persistency of lactation can be defined as the ability of a cow to maintain milk production after peak yield. This parameter was defined in various ways in the literature (Gengler, 1996), with no consensus reached yet on the suitable definition. Lately, this parameter has been calculated as a byproduct of the random regression model (Jamrozik *et al.*, 2002; Druet *et al.*, 2005). In this study, persistency was defined as the breeding value on DIM 280 minus the breeding value for milk yield on DIM 80. DIM 80 was chosen to replace DIM 60 in the definition by Jamrozik *et al.* (1998) because average peak yield occurs in DIM 73 and DIM 65 in Luxembourg and Tunisian Holsteins, respectively (Table 1). Heritability ($h^2_{i(c)}$) for parameter i (daily, 305-d period, and persistency) in country c (Luxembourg or Tunisia) was calculated as:

$$h^2_{i(c)} = \frac{\sigma^2_{a_i(c)}}{\sigma^2_{a_i(c)} + \sigma^2_{pe_i(c)} + \sigma^2_{hy_i(c)} + k * \sigma^2_{e(c)}}$$

The constant k multiplying the residual variance ($\sigma^2_{e(c)}$) takes the values 1, 305, or 2 when heritability is estimated for a given DIM, for a 305-d period, or for persistency, respectively. The additive genetic ($\sigma^2_{a_i}$(c)), PE ($\sigma^2_{pe_i}$(c)), and HY ($\sigma^2_{hy_i}$(c)) variances were computed as: $\sigma^2_{a_i(c)}$ = $\mathbf{q}_i\mathbf{G}_{(c)}\mathbf{q}_i$’, $\sigma^2_{pe_i(c)}$= $\mathbf{q}_i\mathbf{P}_{(c)}\mathbf{q}_i$’, and $\sigma^2_{hy_i(c)}$ = $\mathbf{q}_i\mathbf{H}_{(c)}\mathbf{q}_i$’, respectively, where $\mathbf{q_i}$ is the row vector of the fourth Legendre polynomials associated with parameter i and $\mathbf{G}_{(c)}$, $\mathbf{P}_{(c)}$, and $\mathbf{H}_{(c)}$ are parts of country specific covariance matrices for AG, PE, and HY random regression coefficients, respectively. The vector $\mathbf{q}_{305\text{-d}}$ was calculated as $\sum_{i=1}^{305}\boldsymbol{q_i}$ and that used for persistency ($\mathbf{q}_{\text{pers}}$) was derived as $\mathbf{q}_{280\text{-d}}$ – $\mathbf{q}_{80\text{-d}}$. The genetic correlation between 305-d yield recorded on Luxembourg (l) and Tunisian (t) cows was calculated as:

$$r_{g305(l,t)} = \frac{\mathbf{q}_{305-\mathbf{d}}\mathbf{G}_{(\mathbf{l},\mathbf{t})}\mathbf{q'}_{305-\mathbf{d}}}{\sqrt{\mathbf{q}_{305-\mathbf{d}}\mathbf{G}_{(\mathbf{l},\mathbf{l})}\mathbf{q'}_{305-\mathbf{d}}} \times \sqrt{\mathbf{q}_{305-\mathbf{d}}\mathbf{G}_{(\mathbf{t},\mathbf{t})}\mathbf{q'}_{305-\mathbf{d}}}},$$

where $G_{(l,t)}$ is the genetic covariance matrix of curve parameters for milk yield in Luxembourg and Tunisia, and $G_{(l,l)}$ and $G_{(t,t)}$ are the genetic covariance matrices of the same curve parameters in Luxembourg and Tunisia, respectively. The genetic correlation for persistency was obtained by replacing $q_{305\text{-d}}$ with q_{pers} in the formula above.

Estimated breeding values (EBV) of animals for milk yield at a given DIM (t) were computed as $q_t\hat{a}_s$, where $\hat{a}'_s$ = ($\hat{a}_{0s}$ $\hat{a}_{1s}$ $\hat{a}_{2s}$ $\hat{a}_{3s}$ $\hat{a}_{4s}$) is the vector of solutions for the additive genetic random regression coefficients of animal s. EBV for 305-d milk yield ($\text{EBV}_{305\text{-d}}$) were obtained by summing for each animal the EBV from 1 to 305 DIM. Those of persistency of lactation (EBV_{pers}) were calculated as EBV_{280} – EBV_{80}. Product-moment and rank correlations between EBV of sires with at least 4 daughters with records in each of the 2 countries were calculated using PROC CORR (SAS, 2002).

6.5. Results and Discussion

6.5.1. Production Descriptive Parameters

Parameters describing production systems and milk yield levels in Luxembourg and Tunisia are given in Table 1. Milk production differed between the 2 countries. A first lactating Holstein cow in Luxembourg produced nearly 4 kg more milk per day than her counterpart in Tunisia. This difference summed up to 1,744 kg milk over a whole lactation for all completed lactations in 2004 (ICAR, 2007). Peak yield was also greater for Luxembourg than for Tunisian first lactation cows. Furthermore, primiparous cows in Tunisia tended to reach their peak of production earlier than those under Luxembourg management conditions (Table 1). Zwald *et al.* (2001) found that the number of days to peak yield was larger in countries with a high milk production level than in countries with a low milk production level. The average age at first calving was around 30 months in both populations. While the frequencies of calving were nearly uniform over the year in Tunisia, they were more variable in Luxembourg, with a peak (35%) during September-November and a decline (13%) in the March-May period. Herd sizes were larger in

Tunisia than in Luxembourg, and the average number of recorded cows per herd in Tunisia was 3× higher than that in Luxembourg in 2004 (ICAR, 2007). Luxembourg had a small average number of TD records per herd-test date class (9.4), but this level is in the range found in bordering countries. Herds in Belgium, Netherlands, and Germany, have 5.4, 9.6, and 10.3 records per TD, on average, respectively (Zwald *et al.*, 2001). This same parameter was 36.1 records in Tunisia, comparable to that observed on Israeli (34.0) first lactation Holstein cows (Zwald *et al.*, 2001).

The period of high temperatures lasts from May to September in Tunisia, with peaks during mainly the summer season. High temperature and humidity may compromise milk production of Holstein cows for a long period of time in Tunisia. In Luxembourg, only the month of August may constitute a period of discomfort for Holstein cows because of heat. Negative effects of heat stress on milk production were reported by Ravagnalo *et al.* (2000). Moreover, the average rainfall was greater in Luxembourg than in Tunisia. Limited water resources may constrain the quantity and quality of forage production. This may consequently hinder high yielding breeds from expressing their potentials. Reproduction parameters could also be affected, which would help explain longer calving intervals in Tunisia in 2004 (ICAR, 2007).

Table 2 gives origins of common sires and maternal grandsires for both populations. Luxembourg and Tunisia had 231 common sires, with between 4 and 903 daughters. In addition, 114 maternal grandsires were in common (with at least 4 granddaughters in each country), of which 67 were also common sires. Common sires and maternal grandsires came from the USA, Canada, Germany, the Netherlands, Italy, and France. Sires from the USA and Germany were used the most among all foreign bulls. Nevertheless, some variability was observed in sire usage between the 2 countries (Hammami *et al.*, 2007). The number of daughters from the USA common sires was higher in Tunisia and number of daughters of sires from Germany and the Netherlands was greater in Luxembourg.

***Table 2**. Origin of common sires[1] and maternal-grand-sires[2] (MGS) of daughters with TD records in Luxembourg (LUX) and Tunisia (TUN)*

Country of origin	Sires			MGS		
	n	Daughters (n)		n	Grand-daughters (n)	
		LUX	TUN		LUX	TUN
Canada	18	2895	318	16	2189	161
France	16	516	84	1	4	19
Germany	80	5226	603	23	2648	503
Italy	11	484	203	1	89	116
Netherlands	26	3640	238	10	2333	787
USA	80	1660	4912	63	2216	3086
TOTAL	231	14421	6358	117	9479	4672

[1] *Common sires were defined as sires with at least 4 daughters in each country.*

[2] *Common MGS were defined as sires with at least 4 granddaughters in each country.*

6.5.2. Genetic Parameters

Posterior means of variances for AG, PE, and HY random regression coefficients from within- and between-country analyses are given in Table 3. Estimates obtained for Tunisia in this study were very similar to those for first lactation milk yield obtained by Hammami *et al.* (2008) using a 3-trait-3-lactation random regression TD model. AG variance estimates for the first 3 coefficients from the Luxembourg data were 46 to 69% larger than corresponding estimates from the Tunisian data. On the other hand, Tunisian PE variances for the same first 3 coefficients were 52 to 65% larger than Luxembourg ones. Although the joint analysis provided higher AG and PE variance estimates for the same random coefficients in both countries, proportional differences in these estimates between populations were maintained.

***Table 3**. Posterior means of additive genetic (AG), permanent environment (PE), and herd-year (HY) variances (posterior SD in brackets) of random regression coefficients from within-country and joint analyses for Luxembourg (LUX) and Tunisian (TUN) primiparous Holsteins*

Variance	Country	Within-country					Joint analysis				
		a_0	a_1	a_2	a_3	a_4	a_0	a_1	a_2	a_3	a_4
AG	LUX	4.23 (0.16)	0.39 (0.03)	0.16 (0.01)	0.04 (0.01)	0.02 (0.01)	4.61 (0.17)	0.43 (0.03)	0.20 (0.02)	0.06 (0.01)	0.03 (0.01)
	TUN	1.95 (0.01)	0.23 (0.01)	0.11 (0.01)	0.03 (0.01)	0.02 (0.01)	2.29 (0.16)	0.34 (0.01)	0.13 (0.02)	0.04 (0.01)	0.03 (0.01)
PE	LUX	5.62 (0.12)	1.09 (0.02)	0.47 (0.01)	0.24 (0.01)	0.15 (0.01)	5.81 (0.11)	1.21 (0.02)	0.52 (0.01)	0.28 (0.01)	0.19 (0.01)
	TUN	8.59 (0.01)	1.78 (0.01)	0.91 (0.01)	0.48 (0.01)	0.31 (0.01)	8.66 (0.13)	2.01 (0.03)	0.97 (0.02)	0.49 (0.01)	0.34 (0.01)
HY	LUX	0.26 (0.04)	0.20 (0.01)	0.13 (0.01)	0.05 (0.01)	0.02 (0.01)	0.26 (0.04)	0.22 (0.01)	0.13 (0.01)	0.05 (0.01)	0.02 (0.01)
	TUN	0.48 (0.01)	0.39 (0.01)	0.17 (0.01)	0.06 (0.01)	0.03 (0.01)	0.47 (0.08)	0.33 (0.04)	0.17 (0.01)	0.07 (0.01)	0.03 (0.01)

The largest variances of PE effect in Tunisia could be due to the poor management practices and feeding fluctuations during the year, which introduce additional variation that is permanently associated with each cow compared to its counterpart in Luxembourg. On the other hand, the reduced AG variances in the Tunisian environment can be possibly caused by difficulties encountered by daughters of superior sires to express their genetic potential under harsh conditions. We can speculate that the within-herd correlations of genotype x management (essentially feeding system) in Luxembourg are large because of the available quantity and quality of forages. The most common buffer feeds (i.e., maize silage and brewers grains) used in Luxembourg farms are available only for very few Tunisian farms in limited quantity and with low nutritional values.

Eigenvalues for AG and PE covariance matrices from within-country analyses are shown in Table 4. The first principal component of the AG effect explained 86 and 89% of total variations in milk yield in Tunisia and Luxembourg, respectively. The cumulative proportion of AG variance explained by the first 3 principal components was over 98% of the total variance in each of the 2 countries. However, 4 components were needed to account for that much (98%) of variation in the PE effect. This was in agreement with Pool *et al.* (2000), who reported that a third order Legendre polynomial for AG and a fourth polynomial for PE variances should be used to accurately model variance curves across lactation.

The first 2 components accounted for 97% and 95% of total AG variances in Luxembourg and Tunisia, respectively. These 2 components have been used to represent total yield and persistency in some studies (Jamrozik *et al.*, 2002; Druet *et al.*, 2005). Jamrozik *et al.* (2002) found only small differences with respect to the first 2 principal components among the Australian, Canadian, Italian, and New Zealand Holstein populations when using fourth order Legendre polonomials. Based on a random regression TD model with the same order of Legendre polynomials, Druet *et al.* (2005) found also that the first 2 components explained more than 95% of variation. They used only 2 eigenvectors, associated with the first 2 eigenvalues, as covariates to estimate covariance components of daily milk traits in French Holsteins.

***Table 4**. Eigenvalues (EIG) and their relative proportions (PROP) for additive genetic (AG), permanent environment (PE), and herd-year effect (HY) covariance matrices from within Luxembourg (LUX) and Tunisia (TUN) analyses*

Item		LUX		TUN	
		EIG	PROP	EIG	PROP
AG	1	4.33	0.89	2.01	0.86
	2	0.37	0.08	0.21	0.09
	3	0.11	0.02	0.08	0.03
	4	0.02	0.01	0.02	0.01
	5	0.01	0.00	0.02	0.01
AG	1	5.67	0.75	8.61	0.71
	2	1.07	0.14	1.92	0.16
	3	0.49	0.07	0.97	0.08
	4	0.26	0.03	0.51	0.04
	5	0.08	0.01	0.05	0.01
HY	1	0.37	0.55	0.70	0.62
	2	0.18	0.27	0.24	0.21
	3	0.09	0.14	0.16	0.14
	4	0.02	0.03	0.02	0.02
	5	0.01	0.01	0.01	0.01

In this study (Table 4), a very large proportion of the AG variances (99% for Luxembourg, 98% for Tunisia) was explained by the first 3 eigenvalues, and the relatively small eigenvalues for higher orders show that the rank reduction of the actual model by using only the third order for AG part may be sensible. On the other hand, a relatively smaller proportion of the PE variance (95% for both countries) was explained by the first 3 eigenvalues. These results could indicate that PEs effect should be modeled with at least one order Legendre polynomials more than that for AG effect. The HY effect was intermediate (96% for Luxembourg, 97% for Tunisia) there, it seems that modeling the HY effect could require the same or one order more than that used for the AG effect.

Posterior means of heritability estimates of 305-d yield and persistency as defined in this study for first lactation obtained from univariate and bivariate (Luxembourg and Tunisia used as 2 separate traits) analyses are given in Table 5. Heritabilities obtained from the joint analysis were larger than those obtained from separate analyses. Tunisia had consistently smaller heritabilities than Luxembourg for milk yield and persistency. For instance, heritability for 305-d yield in Tunisia was 53% lower than that in Luxembourg. Ojango and Pollot (2002) reported that heritability estimates for 305-d milk yield in Kenya was 42% lower than that in the United Kingdom when doing a joint analysis. Carabaño *et al.* (1989) found also that Spanish first lactation 305-d milk yield heritability estimated using a sire lactation model (0.16 from within Spain and 0.12 from between Spain and the USA analyses) were smaller than those found in the US population (0.33 from within the US and 0.26 from between Spain and the USA analyses). These authors concluded that low heritability estimates obtained for the Spanish Holsteins were caused by poor management conditions. Differences in heritabilities between Luxembourg and Tunisia may be caused by differences in production levels resulting from differences in climatic conditions and management. Jamrozik *et al.* (2002) also reported variable estimates of lactation curve parameters among countries with different production systems. These authors linked differences in estimates not only to absolute production levels but also to relationships among lactation curve parameters found for any given population. Persistency as defined by Jamrozik *et al.* (2002) clearly depended on production levels of the considered population. Heritability estimates of persistency for both populations were lower than the 0.30 reported by Jamrozik *et al.* (1998) for the Canadian Holsteins using the linear slope between yields at DIM 60 and DIM 280 as a measure of persistency. Low heritability of persistency obtained in Tunisia could reflect difficulties encountered by cows to maintain high milk production after the peak, thereby suppressing expression of genetic variance.

***Table 5**. Posterior means (posterior SD in brackets) of heritabilities (h^2) of 305-d milk yield and persistency[1] of first lactation and correlations[2] between EBV of common sires[3] from within-country and joint analyses in Luxembourg (LUX) and Tunisian (TUN) Holsteins*

Parameters	Within-country analysis				Joint analysis		
	h^2		r_m	r_s	h^2		r_g
	LUX	TUN			LUX	TUN	
305-d milk yield	0.41 (0.01)	0.17 (0.01)	0.38	0.41	0.42 (0.01)	0.19 (0.02)	0.60 (0.03)
Persistency	0.11 (0.02)	0.06 (0.01)	0.27	0.26	0.12 (0.02)	0.08 (0.02)	0.36 (0.04)

[1] *Persistency defined as EBV at DIM 280 – EBV at DIM 80.*

[2] *r_m is the product moment correlation, r_s is the rank correlation, and r_g is the genetic correlation.*

[3] *Common sires were defined as sires with at least 4 daughters in each country.*

Posterior means of genetic correlations for 305-d milk yield and lactation persistency from the joint analysis are shown in Table 5. The genetic correlation between Luxembourg and Tunisian 305-d milk yields (0.60) was low compared to estimates in some studies (Weigel *et al.*, 2001; Jamrozik *et al.*, 2002). Jamrozik *et al.* (2002) reported genetic correlations for total (mostly 305-d) milk yield. Results ranged from 0.66 to 0.83 among Australian, New Zealand, Canadian, and Italian first lactation Holsteins using a random regression TD animal model. Likewise, Weigel *et al.* (2001) reported values greater than 0.80 between total yield correlation estimates obtained by a multi-trait analysis of 16 million first lactation records from 17 Interbull country members. Estimates reported by Weigel *et al.* (2001) were > 0.90 between countries with predominantly grazing systems (Ireland, Australia, and New Zealand). Those correlations were greater than 0.91 among countries with high milk production levels (US, Canada, Belgium, the Netherlands, and Italy). Correlations between total yields in the remaining Interbull countries ranged between 0.80 and 0.90 (Weigel *et al.*, 2001). The genetic correlation between 305-d milk yields in Luxembourg and Tunisia is still in the range of estimates obtained between pairs of countries known with harsh climatic conditions or diverse production systems, e.g., the genetic correlation between the United Kingdom and Kenya was only 0.49 (Ojango and Pollot, 2002). Cienfuegos-Rivas *et al.* (1999) reported a genetic correlation of 0.63 between the USA and Mexico. A slightly larger genetic correlation (0.66) between Italy and New Zealand was reported by Jamrozik *et al.* (2002). The genetic correlation between persistency, as defined in this study, in Luxembourg and Tunisia was 0.36, which is lower than 0.55 obtained between the Canadian and Italian first lactation cows in a study of 4 populations (Jamrozik *et al.*, 2002), where persistency was defined as a by-product of the random regression model. These authors found the lowest estimate (0.16) between the Italian and New Zealand Holsteins. According to Robertson (1959), low genetic correlations suggest evidence of G×E. In this study, low genetic correlations (< 0.80) between parameters (305-d milk yield and persistency) of Tunisian and Luxembourg first lactation indicate that superior animals on a trait in one environment are not necessarily as superior in the other and *vice versa*.

6.5.3. Genotype by Environment Interaction

Genetic variances and heritability estimates revealed unequal genetic expression of Holstein genes under Luxembourg and Tunisian management circumstances. Several studies (Veerkamp and Goddard, 1998; Gengler *et al.*, 2005) reported that the genetic variance for milk yield is greater in high-input systems compared to that in low-input systems. Others (Raffrenato *et al.*, 2003; Ben Gara *et al.*, 2006) found low genetic variance and heritability estimates for production traits under low-input production environments. Low genetic variances for milk yield throughout lactation observed in Tunisian Holsteins translate into smaller differences in breeding values among animals. Performances of cows in Tunisia are limited because of harsh climatic conditions (discomfort) and limited feed resources compared to less constraining factors in Luxembourg where cows are managed under conditions similar to those where their sires were selected. Currently, 70% of total bulls used in Luxembourg cow population were selected in bordering countries with production conditions similar to those found in Luxembourg. Selection responses to the use of US Holstein sires for milk production in

Latin America were estimated to be 53 to 78% of the response observed in the USA (Stanton *et al.*, 1991). The relative response to sire selection expected in Kenya based on United Kingdom breeding values was only about 44% (Ojango and Pollot, 2002). Therefore, environmental factors appear to constrain expression of genetic merit in tropical or subtropical regions relying on imported proven Holstein semen.

Differences in additive genetic variances obtained for Luxembourg and Tunisian populations imply that a scaling effect exists for EBV of sires across these environments. Low genetic and rank correlations translate a re-ranking of sires across these populations. Tunisian EBV of sires for 305-d yields were regressed on corresponding Luxembourg values. Figure 1 shows a plot of these milk yield EBV of the 231 common sires estimated in Tunisia against their EBV in Luxembourg. The slope (b) in the regression equation could be viewed as the expected response measured on daughters in Tunisia from sire selection on EBV in Luxembourg. This regression coefficient was only 0.18 in the current study. This result is less than that (b = 0.32) reported by Ojango and Pollot (2002) from regressing EBV of sires in Kenya on the EBV of the same sires in the United Kingdom.

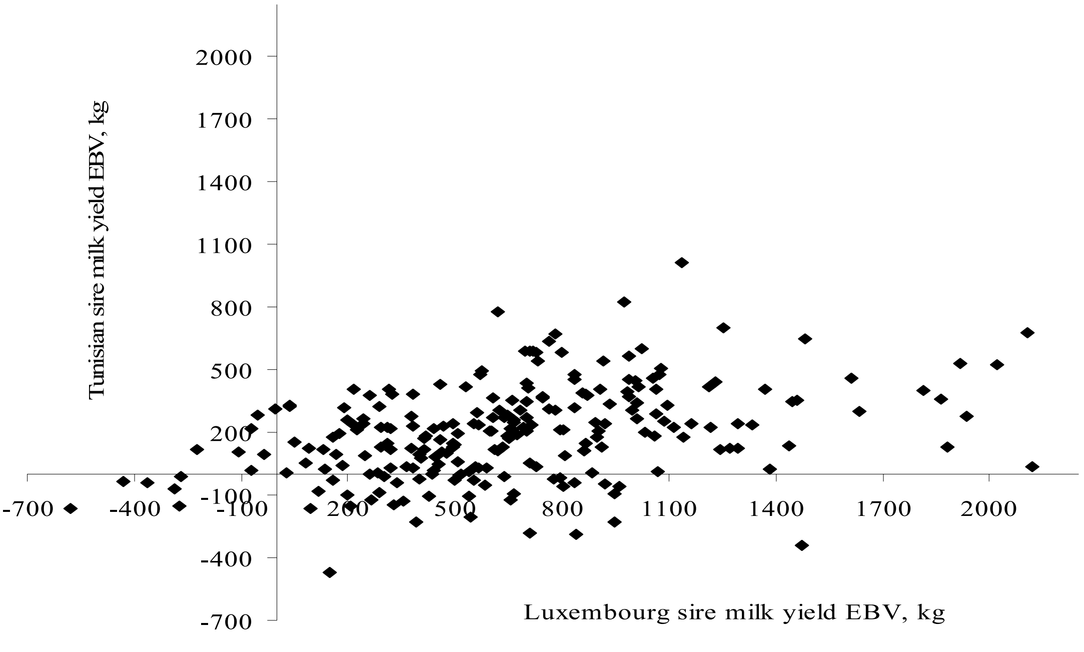

***Figure 1**. Plots of first lactation EBV of common sires, defined as sires with at least 4 daughters in each country, for 305-d milk yield in Tunisia against their EBV in Luxembourg.*

The expected response (b = 0.57) measured on daughters of US sires in the low-input Mexican environment was less than responses of daughters of the same US sires in all US environments (Stanton *et al.*, 1991). These authors concluded that the US Holstein genes had restrained expression under the Mexican management circumstances.

Product moment and rank correlations (Table 5) between $EBV_{305\text{-d}}$ from within-country analyses were lower than corresponding genetic correlations (0.60). Cienfuegos-Rivas *et al.* (1999) found also low rank correlation coefficient (0.59) between herds in low milk production level in Mexico and all herds in the USA. They concluded that this result was evidence for a significant G×E interaction and that sires were ranked differently in the Mexican environment compared to their ranking in the US. Figure 2 shows the $EBV_{305\text{-d}}$ of 15 common sires with more than 30 daughters in Luxembourg. It appears that considerable re-ranking of bulls with respect to milk yield was observed.

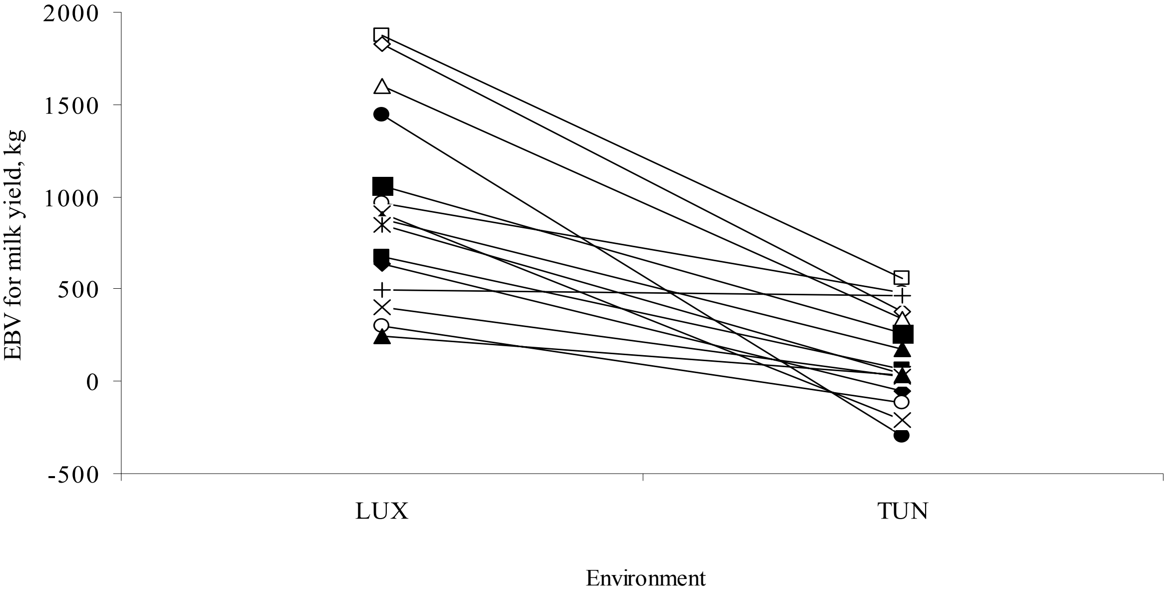

***Figure 2**. EBV for first lactation 305-d milk yield of 15 sires with at least 30 daughters each in Luxembourg (LUX).*

Moreover, product moment and rank correlation based only on these 15 sires were around 0.42. Restricting computation to only this group of sires did not cause any significant change in correlation estimates between EBV found in Luxembourg and Tunisia. Mulder *et al.* (2004) reported that the re-ranking effect is most likely observed with top sires. As on milk yield $EBV_{305\text{-d}}$, there were also differences in the ranking of sires on EBV_{pers} between the 2 environments (Table 6).

Product moment (0.27) and rank correlations (0.26) between EBV_{pers} from within-country analyses were lower than those between $EBV_{305\text{-d}}$ (Table 5). Moreover, the rank correlation between Tunisian sires $EBV_{305\text{-d}}$ and Luxembourg sires EBV_{pers} was 0.21 and that between Luxembourg sires $EBV_{305\text{-d}}$ and Tunisian EBV_{pers} was 0.29. These low correlations indicate that superior animals for 305-d milk yield are not necessarily as superior for persistency of lactation. These results may also imply that animals with high 305-d yield in a favorable environment may have lower yield but greater persistency in a less favorable environment.

Table 6. *Estimated breeding values for 305-d milk yield and persistency[1] of lactation for common sires with more than 30 daughters in Luxembourg*

Sires	Luxembourg			Tunisia		
	305-d milk yield	Persistency	Daughters (n)	305-d milk yield	Persistency	Daughters (n)
S1	1876.99	0.49	31	554.58	0.54	169
S2	1827.43	0.43	113	377.41	0.65	124
S3	1597.63	0.42	35	337.35	0.04	33
S4	1444.13	-0.68	33	-295.79	1.89	56
S5	1063.02	0.96	32	256.88	1.19	410
S6	962.78	-1.38	903	476.42	-0.35	33
S7	910.91	-0.30	132	-209.72	0.15	32
S8	879.55	0.12	235	171.02	0.53	100
S9	850.67	-2.69	660	39.92	-0.70	29
S10	677.83	0.04	227	67.29	0.80	26
S11	634.24	-0.46	512	-54.28	0.05	44
S12	495.16	0.13	91	464.65	0.12	93
S13	401.77	0.03	297	23.99	0.47	20
S14	297.56	-0.19	71	-116.09	-1.11	35
S15	247.01	-1.19	227	29.81	-0.75	52

[1] *Persistency was defined as EBV at DIM 280 – EBV at DIM 80.*

In general, results from this study indicated potential interactions between genotype and environment for 305-d milk yield and persistency in Holsteins. That is, potential benefits from importing superior germplasm would be reduced in limited input production systems. Peterson (1988) reported that a re-ranking effect was observed for Canadian sires when used in New Zealand. The authors suspected this is caused by the reduced ability of daughters of Canadian sires to get sufficient energy intakes from exclusive pasture regimes in New Zealand. Cienfuegos-Rivas *et al.* (1999) concluded that significant G×E was found for milk yield using Mexican and US Holsteins. These authors reported that only cows in low US producing environments were able to predict performances of their paternal half sisters in Latin American countries in agreement with reports by Stanton *et al.* (1991) and Costa *et al.* (2000). They also suggested that investing in imported semen without testing this germplasm under local circumstances is probably inappropriate in certain low-input environments.

6.6. Conclusions

Genetic parameters of lactation curves were obtained from single and joint analyses of Luxembourg and Tunisian data by a random regression TD animal model using a fourth order Legendre polynomial. AG variance estimates from the Luxembourg data were larger than corresponding estimates from the Tunisian data while Tunisian PE variances were higher than Luxembourg ones, reflecting differences in production levels and environments. Genetic parameters of lactation curves revealed differences in gene expressions between Luxembourg and Tunisian Holsteins. A high heritability for 305-d milk yield and a moderate one for persistency found in Luxembourg Holsteins give more possibilities for selection and genetic progress under their producing environments. On the other hand, the Tunisian constraining conditions including climatic, health stressors, and feeding limitations impede the expression of superior genes for milk production and thus may reduce potential gains from selection. Genetic correlations between Luxembourg and Tunisia for 305-d milk yield and persistency were in the same range as estimates obtained between pairs of countries known for important differences in climates and production systems. Rank correlations and regression coefficients obtained on sires EBV for milk yield from within Luxembourg and Tunisia analyses were lower than genetic correlations found by the joint analysis. Low correlations are evidence for G×E. Moreover, sires used in Luxembourg and Tunisia were ranked differently in the 2 environments. Results suggest that Holsteins selected in favorable environments will not perform as well in less favorable management conditions. They also suggest that low- to medium-input production systems should consider the use of semen of sires selected in regions with low to medium producing environment in countries with leading dairy industries if they were not able to select from own populations. Finally, even if rankings between animals might change by going from one environment to the other; the correlations estimated across countries were positive, and the greater selection intensity in temperate regions still likely makes these animals genetically superior for milk yield, on average, even in different environments, provided that sufficient feeding and management are provided. However results (i.e., $r_g \leq 0.60$) showed that paying premium prices for elite animals from temperate environments or semen from those animals is not necessarily a good strategy. The issue is to transfer correctly the genetic progress from temperate high-input levels into different environments. Moreover, importing countries should employ more efforts to meet the elementary needs of high yielding breeds under their conditions.

6.7. Acknowledgments

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Results obtained in Chapter 6 agree with those presented in Chapter 5. Both showed that significant G x E was detected for milk yield and persistency between Luxembourg and Tunisia. They considered the whole country as a specific environment identifying Luxembourg as a high-input system but Tunisia as a low- to medium input system. However, some herds in the two countries can be regarded as similar to each other in management, production system, and genetic composition more than some herds within each of the two countries. Quantifying the magnitude of the G x E interaction among various environments in each country should be more opportune but depends on the availability of accurately quantifiable environmental descriptors. Environmental factors that cause re- ranking have been mainly related to feeding levels and systems, climate, and herd size. Random regression TD models recently employed by the majority of countries for the genetic evaluation offer more adequate means to depict variations in each herd from month to another. Solutions from herd-test-date fixed effect give good idea about the feeding and management levels. The last parameter was used in the next Chapter to cluster three management levels in each country. Genetic correlations within- and across-environments were used to appreciate the selection response in each specific-environment. Differential selection based on HM criterion was tested. ***The next chapter summarizes results on environmental sensitivity for milk yield in Luxembourg and Tunisian Holsteins using HM levels, results were submitted as an original paper to the Journal of Dairy Science.***

Chapter 7

Environmental Sensitivity for Milk Yield in Luxembourg and Tunisian Holsteins Using Herd Management Level

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7.1. Interpretive Summary

Dairy herds in Luxembourg and Tunisia were classified into high, medium, and low opportunity production environments. Milk production and genetic parameters were affected by the herd management level. The highest milk yields and additive genetic variances were found in herds with better management practices and resources. Superior genes for milk yield in favorable environments did not perform satisfactorily in less favorable environments. Genetic exchange between high and low input milk production environments should be done carefully.

7.2. Abstract

Milk production data of Luxembourg and Tunisian Holstein cows were analyzed using herd management (**HM**) level. Herds in each country were clustered into high, medium, and low HM levels based on solutions of herd-test-date and herd-year of calving effects from national evaluations. Data from both populations included 730,810 test-day (**TD**) milk yield records from 87,734 first-lactation cows. A multi-trait, random regression, TD model was used to estimate (co)variance components for milk yield within- and across-country HM levels. Additive genetic and permanent environmental variances of TD milk yields varied with management level in Tunisia and Luxembourg. Additive variances were smaller across HM levels in Tunisia than in Luxembourg, whereas permanent environmental variances were larger in Tunisian HM levels. Highest heritability estimates of 305-d milk yield (0.41 and 0.21) were found in high HM levels, while lowest estimates (0.31 and 0.12, respectively) were associated with low HM levels in both countries. Genetic correlations among Luxembourg HM levels were over 0.96, whereas those among Tunisian HM levels were below 0.80. Respective rank orders of sires ranged from 0.73 to 0.83 across Luxembourg environments and from 0.33 to 0.42 across Tunisian HM levels indicating high re-ranking of sires in Tunisia and only a scaling effect in Luxembourg. Across-country-environment analysis showed that estimates of genetic variance in the high, medium, and low classes of Tunisian environments were 45, 69, and 81% lower, respectively, than the estimate found in the high Luxembourg HM level. Genetic correlations among 305-d milk yields in Tunisian and Luxembourg HM environments ranged from 0.39 to 0.79. The largest estimated genetic correlation was found between the medium Luxembourg and high Tunisian HM levels. Rank correlations for common sires' estimated breeding values (EBV) among HM environments were low and ranged from 0.19 to 0.39 implying the existence of genotype by environment interaction. These results indicate that daughters of superior sires in Luxembourg have their genetic expression for milk production limited under Tunisian environments. Milk production of cows in the medium and low Luxembourg environments were good predictors of that of their paternal half-sisters in the high Tunisian HM level. Breeding decisions in low input Tunisian opportunity environment should utilize semen from sires

with daughters in similar production environments rather than semen of bulls proven in higher management levels.

Keywords: Environmental sensitivity, genotype by environment interaction, genetic correlation, herd management level.

7.3. Introduction

The ability of a genotype to alter phenotypic expression in response to environmental differences is known as phenotypic plasticity or environmental sensitivity (Falconer and Mackay, 1996). In animal breeding, genetic variation in response to environmental differences is used as a definition of genotype by environment interaction (**G×E**). Investigations on G×E within- and across-countries have been mostly based on the region or country border as a criterion for global environmental definition (Carabaño *et al.*, 1989; Carabaño *et al.*, 1990; Schaeffer, 1994; Rekaya *et al.*, 2001; Ojango and Pollot, 2002; Fikse *et al.*, 2003a; Hammami *et al.*, 2008). However, environments across countries could be more similar than those within countries; and herds from different countries can share similar environmental characteristics compared to herds within the same country. Clustering of herds across countries using descriptive variables and ignoring country borders has been implemented in other studies (Weigel and Rekaya, 2000; Fikse *et al.*, 2003b; Zwald *et al.*, 2003; Cerón-Muñoz *et al.*, 2004).

Experimental studies investigated G×E where environments were designed to differ with respect to feeding levels and systems (Veerkamp *et al.*, 1995; Kolver *et al.*, 2002; Beerda *et al.*, 2007). In general, using experimental herds with good quality data to assess G×E is more illustrative, but is expensive and difficult to realize especially in developing countries. To overcome the lack of information about environmental characteristics, some proxies to the feeding level and management were used to form homogenous environments in studies on G×E in tropical and temperate regions. Herds were stratified by mean herd milk yield level (Kolmodin *et al.*, 2002; Hayes *et al.*, 2003; Berry *et al.*, 2003) or by within-herd milk yield standard deviation (**HYSD**) (Stanton *et al.*, 1991; Cienfuegos-Rivas *et al.*, 1999; Costa *et al.*, 2000; Raffrenato *et al.*, 2003). Most studies on G×E by character state or reaction norm models (Stanton *et al.*, 1991; Weigel and Rekaya, 2000; Kolmodin *et al.*, 2002; Raffrenato *et al.*, 2003) used lactation records. Computing facilities have lead to the use of test day (**TD**) models worldwide in genetic evaluations. The use of TD records improved the accuracy of estimated breeding values (**EBV**). Hayes *et al.* (2003) reported that TD records are better suited to investigate within- and between-cow variations at different environments than lactation yields because they better account for environmental effects peculiar to each TD throughout the lactation.

In Tunisia, Holsteins are mostly managed on small farms with little to no land. Nevertheless, large-scale farms exist and are located in the north of the country. Farms present a wide range of environments and intensity of production varying from intensive to extensive systems. Herds differ also with respect to health care, feed resources, and feeding system within- and across-production sectors. Rekik *et al.* (2003) reported that the effect of production sector was highly significant on lactation curve parameters in Tunisia. Mean milk yield in 305 days ranged from 5456 kg in cooperative herds to 8337 kg in private herds.

As in most European countries, dairy farms in Luxembourg can be summarized as high input production systems. Feed resources are varied; and they are supported by relatively high use of fertilizers, buffer feeds (i.e., maize silage and brewers grains) and concentrates, which are usually fed to improve milk production (Van Arendonk and Liinamo, 2003). Grazing is wide spread in Luxembourg where climatic and pedological conditions favor the development of naturally dominant meadows and pastures. Organic farming, with fodder grass being the organic product of choice, is gaining popularity in Luxembourg as a low-input form of dairy herd management (**HM**) where reduced costs of feeding and equipment may lead to greater net profit even if milk production is decreased.

In a previous study, Hammami *et al.* (2008) found evidence of a large G×E for milk yield and persistency using Luxembourg and Tunisian Holstein populations where lactation performance in each country was considered as a different trait and the country border delimitation was defined as an environmental criterion. However, these authors did not account for differences between herds in management practices within country or how genotypes respond to HM level within these 2 geographically distinct environments. Calus *et al.* (2002) suggested that clustering herds in groups of similar production systems or intensity of production might be more effective to investigate G×E effects than only considering sire-herd-year-season differences. Fikse (2004) reiterated that breeding programs should have more advantages when the international genetic evaluation is run using performance records in a production system rather than on a country basis. Furthermore, the environmental definition and the heterogeneity of variance may affect the magnitude of G×E and therefore genetic evaluation and selection accuracy.

The assumption of homogeneous variance across herds with different management levels has no major effect on the evaluation of sires when the latter are equitably used in those herds and that heritability is greatest in the more variable environment (Vision, 1987; Boldman and Freeman, 1990). Otherwise, ignoring the heterogeneity of variance can lead to bias in genetic evaluations. This bias may have severe consequences as the intensity of selection increases and might then limit the effectiveness of breeding programs (Hill, 1984; Vision, 1987). Fahey *et al.* (2007) investigated the effect of heteroscedasticity on genetic parameter estimates for production traits between grazing and confinement herds in the US to ascertain if that unmasked underlying G×E effects. They found only modest evidence for G×E that did not arise solely from heteroscedasticity. Raffrenato *et al.* (2003) reported that clustering Sicilian herds on management level was effective in identifying heterogeneous genetic variance. Breed differences in environmental sensitivity to micro- and macro-environmental change could be detected by the examination of heterogeneity of variance (Lynch and Walsh, 1998). Quantifying the environmental sensitivity of dairy sires in different environments is important for making breeding decisions and implementing efficient selection strategies suitable for each specific environment. This can allow the differentiation of sires ranking similarly (desirable) across different herd environments from those ranking differently in one specific environment versus another.

There are differences in management practices between and within herds in Luxembourg and Tunisia. These within and across-country differences may be associated with heterogeneous genetic parameters. It is also important to determine if sires can be used throughout the whole of each country independently of management level. Grouping herds on HM level ignoring country borders may be advantageous and could better accommodate G×E within- and across-country environments. Therefore, the main objective of this study was to evaluate the environmental sensitivity for milk yield in Holsteins using HM levels within and between Luxembourg and Tunisian contrasted environments.

7.4. Materials and Methods

7.4.1. Data

A total of 730,810 TD milk records of 87,767 primiparous Holstein cows collected between 1995 and 2006 were used. Luxembourg data were provided by VIT (Vereinigte Informationssysteme Tierhaltung, Verden, Germany). Tunisian data were provided by the Center for Genetic Improvement of the Livestock and Pasture Office. Data included records in herds having at least 4 daughters of sires common to both cow populations. Details on data structure are found in Hammami *et al.* (2008). A pedigree file dating back to 1927 was obtained for all animals in the analysis. There were 2,546 and 2,035 sires with daughters having records in Luxembourg and Tunisia, respectively. Among those sires with progeny records, 231 bulls had daughters in both countries (14,421 and 6,358 daughters in Luxembourg and Tunisia, respectively).

7.4.2. Definition of Environment

Nearly all studies investigating environmental sensitivity in dairy cattle within- or across-countries reported that even if no direct measures of nutrition and feeding were available, herd parameters linked to nutrition were the most important for G×E (Calus and Veerkamp, 2003; Zwald *et al.*, 2003; Cerón-Muñoz *et al.*, 2004; Haskell *et al.*, 2007). In this study, because of the lack of information about feeding levels and systems, it was assumed that management group solutions from a genetic analysis of milk yield would reflect general HM level. In order to assess the environmental sensitivity within and across Luxembourg and Tunisian environments, the following steps were applied to determine environmental (HM) differences.

Herd management estimation. Data were analyzed using the following (in matrix notation) random regression (**RR**) TD model:

$$\mathbf{y = Xb + Q\,(Za + Zp + Wh) + e}$$

where **y** is a vector of TD milk yield records**, b** is a vector of fixed effects: herd-test-date, age within season of calving and classes of 25 DIM, and stage of lactation classes of 5 DIM, **a** is a vector of RR coefficients for the animal additive genetic (**AG**) effect**, p** is a vector of RR coefficients for permanent environmental (**PE**) effect**, h** is a vector of RR coefficients for herd-year of calving common environmental effect (**HY**)**, e** is a vector of residual effects, **Q** is a matrix of Legendre polynomials, and **X**, **Z,** and **W** are incidence matrices relating observations to the various effects. Legendre polynomials were third-order for AG and HY effects and fourth-order for the PE effect. Higher order polynomials for PE effect were used following recommendations by Hammami *et al.* (2008), who reported that AG and HY in this data are sufficiently modeled by third-order Legendre polynomials, whereas fourth-order polynomials were necessary to better fit the PE effect.

First, solutions for herd-test-date and herd-year of calving effects were obtained for Luxembourg and Tunisian cows. These solutions were then summed up for each cow within a herd to define the management level for each TD record, and the average of cows' levels in a herd defined the mean management level for that herd in Luxembourg or in Tunisia. These mean management levels were then the basis for clustering herds into HM levels within country.

Contrasting herd environments. C lustering was applied to find similarities between herds within each country environment defined as explained before. The procedure CLUSTER (SAS, 2002) with Ward's minimum variance was used. The standard option was employed to standardize the HM (mean = 0 and standard deviation = 1). Three different levels of management were obtained based on the pseudo F statistic for each country. They will be hereafter referred to as high, medium, and low HM levels. Descriptive statistics on these management classes in addition to other characteristics of Luxembourg and Tunisian environments are in Table 1. Total number of sires used in each of the 2 environments, the number of sires in common, and the total number of common daughters between pairs of HM within- and across-countries are in Table 2.

7.4.3. Analysis

A multiple trait RR TD model was used to estimate (co)variance components for milk yield within and across Luxembourg and Tunisian HM levels. Fixed and random effects were similarly defined as in the model used for HM estimation but were nested within contrasted environments. This model was used to estimate genetic parameters and breeding values. The covariance structure was:

$$V\begin{bmatrix}\mathbf{a}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{G} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{P} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix},$$

where $\mathbf{G} = \mathbf{A} \otimes \mathbf{G_0}$, $\mathbf{P} = \mathbf{I} \otimes \mathbf{P_0}$, $\otimes$ denotes the Kronecker product; **A** = the additive genetic relationship matrix; $\mathbf{G_0}$ = 18 × 18 covariance matrix for AG regression coefficients; and $\mathbf{P_0}$ = 24 × 24 covariance matrix for PE regression coefficients. All across-country environmental covariances in $\mathbf{P_0}$ were equal to zero because these effects were considered independent across-country environments. **I** = identity matrix. The matrix **R** was considered to be diagonal as $\mathbf{I}\sigma^2_i$, where σ^2_i = residual variances for milk yield for each of the 6 environments (i = 1 to 6).

Table 1. *Description of data and mean milk yield and standard deviation (in parentheses) for different lactation phases by herd management level (high, medium, or low) in Luxembourg and Tunisia*

	Luxembourg			Tunisia		
	high	medium	low	high	medium	Low
Test-day records	151,587	192,005	121,430	122,825	57,723	85,240
Number of cows	18,285	22,446	13,939	15,218	7,324	10,555
Number of herds	179	106	142	31	29	38
Herd management (kg)	9.6 (2.7)	6.8 (2.6)	4.2 (2.7)	6.8 (4.6)	5.9 (4.1)	4.5 (3.8)
Daily milk yield (kg)	25.5 (2.7)	22.4 (5.3)	19.5 (4.9)	21.6 (6.1)	17.7 (5.3)	13.7 (4.4)
Age at calving (month)	29.4 (3.6)	30.5 (3.6)	31.5 (3.7)	28.6 (3.5)	30.5 (5.9)	29.3 (3.9)
Milk at DIM 80 (kg)	28.1 (4.7)	25.2 (4.7)	21.7 (4.6)	24.8 (6.0)	19.3 (4.9)	15.6 (3.9)
Milk at DIM 280 (kg)	21.8 (5.0)	18.7 (4.2)	16.1 (4.0)	17.9 (5.4)	14.9 (4.8)	12.0 (3.8)
Test day records per herd-test-date classes	12.1 (8.7)	8.8 (5.1)	7.5 (4.0)	60.1 (57.6)	26.8 (23.1)	27.8 (16.5)
305-d milk yield* (kg)	7917 (1248)	7017 (1085)	6086 (969)	7375 (1555)	5462 (1252)	4623 (1027)

** Actual 305-d milk yield*

Table 2. *Total number of sires used in each herd management level group (on diagonal), sires with at least 4 daughters in common between each pairs of environments (above diagonal), and total number of daughters in common across pairs of environments (below diagonal)*

	Luxembourg			Tunisia		
	high	medium	Low	high	medium	Low
Luxembourg						
high	1,663	565	471	126	102	49
Medium	32,242	1,547	614	115	99	45
Low	23,861	42,620	1,175	100	82	37
Tunisia						
high	7,489	5,608	3,982	1,335	208	185
medium	4,904	4,511	3,402	16,199	763	170
Low	2,593	1,719	1,041	18,000	14,096	648

Genetic and non-genetic parameters were estimated with a Bayesian approach via a Gibbs sampling algorithm (Misztal *et al.*, 2002). A chain of 250,000 samples (with 50,000 as burn-in period) was generated. Convergence of Gibbs chains was monitored by inspecting plots of selected realizations. Variances, heritabilities, and correlations for 305-d yields were calculated following Hammami *et al.* (2008). Genetic correlations were computed among TD milk yields recorded in various HM levels. Rank correlations between EBV of common sires estimated separately in each of the 6 environments were used to assess the level of re-ranking of sires in different environments. Rank correlations were calculated using PROC CORR (SAS, 2002) for common sires that had at least 30 daughters in within-country environments and at least 4 daughters in common in across-country environments. Coefficients of correlated responses in low environments from sire selection in high environments were estimated to evaluate using semen from sires proven in high HM herds to improve milk production in low HM levels. They were obtained by regressing EBV of common sires between pairs of contrasted environments within each country.

To investigate the possibilities of using a selection differential and to differentiate between sires ranking similarly across various herd environments (desirable) and those ranking high only in specific environments (undesirable), firstly a national evaluation was performed for each country; and their top 20 national sires were identified. Second, a separate evaluation for each of the 6 specific environments studied was performed; and the top 20 sires in each specific environment were obtained. Desirable sires were those with similar average EBV from national and country specific environments evaluations, signaling that when they are the top nationally they are still the top in each of the country specific environments.

7.5. Results and Discussion

7.5.1. Within-country-environment analysis

Table 3 has estimated AG and PE variances and heritabilities for 305-d milk yield in contrasted Luxembourg and Tunisian environments. Estimates of AG and PE variances decreased from the high to the low HM level in both countries. The increase in AG and PE variances with HM level found in this study for both populations is in accordance with results in other studies (Stanton *et al.*, 1991; Cienfuegos-Rivas *et al.*, 1999; Costa *et al.*, 2000; Raffrenato *et al.*, 2003) that used HYSD of mature equivalent milk yield to stratify herds. The TD model used in this study accounts for short time environmental variation (month-to-month) unlike the herd-year classification of management groups in the lactation model. Moreover, the sum of the herd-TD and herd-year solutions from the TD model may provide an efficient HM level descriptor independent of the other fixed effects in the model.

Heritability estimates for 305-d milk yield were larger in the 3 Luxembourg contrasting environments than estimates in respective Tunisian HM levels (Table 3). The results, on heritability estimates in herds with varying milk production levels, are in agreement with those reported in other studies (Hill *et al.*, 1983; Boldman and Freeman, 1990; Castillo-Juarez *et al.*, 2000). Large heritability estimates for milk yield in high HM levels reflect high genetic variation of milk production by cows in this HM class compared to that of their contemporaries in the low HM level.

Table 3. *Posterior means (and SD) of estimates of 305-d milk for additive genetic (AG), permanent environmental (PE) variances, and heritability within-country and herd management (HM) levels*

HM levels	Luxembourg AG variances	Luxembourg PE variances	Luxembourg heritability	Tunisia AG variances	Tunisia PE variances	Tunisia heritability
High	496,169 (20,137)	645,987 (16,827)	0.41 (0.02)	272,794 (25,214)	952,796 (32,591)	0.21 (0.02)
Medium	339,274 (14,079)	537,194 (11,730)	0.37 (0.01)	151,628 (22,947)	764,791 (28,154)	0.15 (0.03)
Low	203,808 (13,789)	422,877 (11,702)	0.31 (0.02)	96,568 (11,425)	595,144 (12,604)	0.12 (0.03)

The high Tunisian HM class included large herds with more milk yield (Table 1) where cows are fed with concentrates, silage, oat hay, and green forage. Large herds were also found to be associated with large AG and PE variances for milk yield in other populations (König *et al.*, 2005; Gernand *et al.*, 2007). On the other hand, the low HM included mostly small herds where cows are fed by-products, low quality oat hay, and moderate quantities of concentrates bought from the market. High and medium Tunisian HM levels could be compared to conventional systems found in temperate regions. Thus, high performance levels could be reached when limiting environmental effects are better controlled unlike in low HM, where milk production levels as well as AG and PE variances were reduced.

In Luxembourg, feeding resources, heat stress, health care, and financial capacities are not constraining factors for milk production. Dairy farming in Luxembourg varies from conventional to grazing with at least 4 months outdoors where cows obtain forage from pasture. Heritability estimates for milk yield obtained in Luxembourg for high and low HM levels were in the same range of estimates found in conventional and grazing farms in Canada (Boettcher *et al.*, 2003).

Genetic correlations for milk yield among contrasted environments (Table 4) were different between the 2 countries. In Luxembourg, genetic correlations among all pairs of HM classes were greater than 0.96 suggesting that sires will rank similarly in the 3 HM levels in Luxembourg. Correlation coefficients in Table 4 (from 0.73 to 0.83) indicate minimal re-ranking of sires among these Luxembourg HM levels. However, differences in variance estimates across these HM classes may lead to scaling effects in sires' EBV, especially between low and high HM levels. Kearney *et al.* (2004) reported a genetic correlation of 0.94 between lower quartiles in conventional and grazing US herds where mean milk yields (mature equivalent) were 6,435 and 7,925 kg in grazing and conventional herds, respectively, which is in the same range of 305-d yields (6,086 and 7,917 kg) recorded in the low and high HM levels in Luxembourg. Boettcher *et al.* (2003) also found a genetic correlation of 0.93 between milk yields in conventional and grazing Canadian herds.

***Table 4**. Posterior means (and SD) for genetic (above diagonal), and rank correlations[1] (below diagonal) for 305-d milk yield within- and across-country herd management levels in Luxembourg and Tunisia*

		Luxembourg			Tunisia		
		High	Medium	Low	High	Medium	Low
Luxembourg	High		0.98 (0.00)	0.97 (0.01)	0.61 (0.09)	0.43 (0.11)	0.39 (0.12)
	Medium	0.82		0.97 (0.01)	0.79 (0.05)	0.70 (0.10)	0.43 (0.10)
	Low	0.76	0.83		0.77 (0.06)	0.67 (0.10)	0.55 (0.09)
Tunisia	High	0.41	0.43	0.26		0.78 (0.04)	0.70 (0.05)
	Medium	0.38	0.34	0.23	0.42		0.73 (0.05)
	Low	0.26	0.39	0.19	0.33	0.37	

[1] *Rank correlation estimated between EBV of common sires of each pairs of environments from separate evaluation.*

Genetic correlation estimates among milk yields in different HM levels in Tunisia were lower than the threshold of 0.80 suggested by Robertson (1959), indicating the presence of G×E. These coefficients ranged from 0.70 (between high and low HM levels) to 0.78 (high and medium HM levels). Rank correlation coefficients among EBV of common sires in the 3 Tunisian HM levels ranged from 0.33 to 0.42, indicating a high potential for re-ranking of sires among these 3 contrasted environments. Low genetic correlations for milk yield obtained among Tunisian HM classes are in the same range of those found in high and low environments in the Sicilian region of Italy (Raffrenato *et al.*, 2003). These authors suggested a major re-ranking of sires among the various environments defined in their study using HYSD of milk yield to classify herds.

***Table 5**. Estimated correlated response[1] in milk yield from selection within contrasted environments in Luxembourg and in Tunisia*

	High (X) – medium (Y)	High (X) – low (Y)	Medium (X) – low (Y)
Luxembourg	0.69	0.53	0.59
Tunisia	0.39	0.16	0.17

[1] *Correlated responses to selection were determined by regressing EBV of common sires (Y) in one herd management level (medium or low HM) on EBV of common sires in other HM (high or medium) levels (X) within each country.*

Coefficients of correlated response in medium and low HM levels from selection in high or medium HM within Luxembourg and Tunisian environments are in Table 5.

Daughter responses in both countries were greatest in high HM and least in low HM levels. However, there were clear differences with respect to the level of genetic response between the 2 countries, in favor of selection for milk yield in Luxembourg. In Tunisia, the highest regression coefficient was 56% lower than its corresponding value in Luxembourg. Correlated responses for milk yield in Luxembourg HM classes were consistent with findings from across-country analyses (Stanton *et al.*, 1991; Cienfuegos-Rivas *et al.*, 1999; Castillo-Juarez *et al.*, 2000; Costa *et al.*, 2000; Rafrenato *et al.*, 2003; Verdugo *et al.*, 2004).

Results in Table 6 compare average EBV for the top 20 sires where national data were used for genetic analysis to average EBV for the top 20 sires where data from only one specific environment were considered for genetic analysis. The resulting absolute differences in average merit between the Luxembourg national top 20 sires and the top 20 sires identified in the either high or low Luxembourg specific environment was the lowest. This indicates that the best national 20 sires were also the best ones in this specific environment. Moreover, 18 and 12 of these sires remained in the top 20 identified using specific environment evaluations in high and low HM levels in Luxembourg, respectively. In contrast, ranking of sires in Tunisia changed between national and the 3 specific environment evaluations.

Table 6. *Average EBV of the national[1] top 20 sires, the specific environment[2] (SPE) top 20 sires and the average number of daughters per sire for the 2 extremes herd management (HM) environments in Luxembourg and Tunisia*

	Luxembourg				Tunisia			
	National Top 20		SPE Top 20		National Top 20		SPE Top 20	
Environments	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire
High HM	1689	91	1731	88	836	90	990	104
Low HM	1233	76	1098	71	613	93	309	92

[1] *average EBV of the top 20 sires evaluated using the whole performance data of each country.*
[2] *average EBV of the top 20 sires evaluated using performance data specific to each herd management within each country.*

There were 16 of the 20 top national sires that ranked high in the high HM level evaluation, but only 2 of the top 20 sires ranked by the specific low HM environment were found in the Tunisian national top 20 sires list. Nevertheless, the number of daughters per sire within a specific environment should be taken into account when comparing between national and specific environment evaluations. Luxembourg breeders may use sires progeny tested in various HM levels without great risks. However, semen exchange among Tunisian HM classes should be used only with caution because differences in management practices and resources among those management classes may lead to genetic re-ranking. By limiting restrictions that foster G×E, it is possible to get more benefits from imported semen for usage in the high and medium HM environments. Because imported semen is often expensive, it is very difficult to get efficient economic returns from imported germplasm in the low Tunisian HM level. A specific breeding strategy for this large class of herds in the country could be implemented to rely on semen of bulls progeny tested in herds at the same management level, probably requiring reliance on progeny testing in local herds.

7.5.2. Across-country-environment analysis

Genetic correlations of first lactation milk yield in the high Luxembourg HM level with milk yield in the high, medium, and low Tunisian HM levels were low (Table 4). These coefficients were higher among similar (0.61) than among divergent (0.39) HM levels. Thus, severe re-ranking of sires of the high HM level in Luxembourg with the 3 Tunisian environments has occurred. These low genetic correlations were the consequence of reduction in genetic variances in the Tunisian environments (Table 3) reflecting differences in HM value and milk yield observed between the high Luxembourg and high Tunisian HM levels (Table 1). Similar declines in genetic correlation estimates with increased differences in management levels were reported in other studies (Cromie *et al.*, 1998; Kearney *et al.*, 2004). Genetic correlations between medium Luxembourg and high, medium, and low Tunisian HM levels (Table 4) were below 0.80. The highest correlation (0.79) was observed between the medium Luxembourg and high Tunisian HM levels. Moreover, AG variance of milk yield in the medium Luxembourg HM level was only 21% larger than that found in the high HM environment in Tunisia (Table 3). Nevertheless, given the low rank correlations between EBV of common sires in the contrasted environments (Table 4), re-ranking of sires on EBV has occurred even between the medium Luxembourg and high HM classes. Cienfuegos-Rivas *et al.* (1999) found that the largest genetic correlation was obtained between the low US and high Mexican environments that had similar mean HYDS. They also reported that the proportion of US genetic superiority that was recovered in the high HYSD Mexican environments when sires were selected on their daughters' performances in all US environments were only 80% effective when US sires were evaluated in the US low opportunity environment. Genetic correlations for milk yield between low Luxembourg HM and high, medium, and low Tunisian HM levels (Table 4) were similar to those obtained between the medium in Luxembourg and the 3 Tunisian HM levels. Generally, results in this study suggest that daughter performances in the medium and low Luxembourg HM levels could be considered good predictors of their paternal half-sister performances in the high HM levels in Tunisia. Genetic correlation estimates for across-country HM levels from the current data should be taken with caution because of the low number of common bulls with more than 20 daughters in the different contrasted environments within country.

Genetic correlations of milk yield estimated across-country and environments were below 0.80. Correlations found between the medium and low Luxembourg and the high Tunisian environments were approximately 0.80. On the other hand, genetic correlations among all of the Luxembourg environments and the low Tunisian environment were below 0.60, suggested by Mulder *et al.* (2006) as a break-even point for separate breeding schemes for similarly defined environments. Milk yield genetic correlations among various HM levels indicate that sires will rank differently between Luxembourg and Tunisian environments. Hammami et al (2008) found evidence for G×E for milk yield using within and across-country analyses of Luxembourg and Tunisian data where each country was treated as a unique and constant production environment. Genetic correlations for 305-d milk yield and persistency between countries were 0.60 and 0.36. It was not possible from that study to compare genotypes' performances in across and within- country specific environments with varying HM levels to explore possibilities for semen exchange among production systems rather than between populations. Results from Hammami *et al.* (2008) and the present study suggest that management levels in addition to climatic conditions are potential sources of G×E effects.

In addition to differences in management resources between Luxembourg and Tunisia, Holsteins may not tolerate extended heat stress in Tunisia. Furthermore, low HM herds are frequent in Tunisia. Locally evaluated Tunisian bulls should be more suitable for this group of herds. Vargas and van Arendonk (2004) compared genetic gain of a local progeny-testing scheme in Costa Rica with genetic gain of semen importation from the United States. They concluded that given the genetic correlation between the 2 countries was around 0.60, a local breeding program based on a nucleus herd could be more profitable than a strategy based on continuous semen importation.

7.6. Conclusions

The emphasis in this study was on milk yield of first lactation Holstein cows in response to management levels within and across Luxembourg and Tunisian production environments. Genetic parameters were dependent on HM levels in Luxembourg and Tunisia. Within-country-environment genetic correlations of milk yield suggest that there was insufficient sire ranking in Luxembourg to warrant formation of separate breeding schemes for their contrasted environments. However, low genetic and rank correlations within the Tunisian environments indicate serious re-ranking of sires among HM levels. Genetic correlations between medium and low Luxembourg and high Tunisian HM levels were close to 0.80 supporting the hypothesis daughters producing in those 2 Luxembourg environments could be considered as a good performance predictor of their paternal half-sisters in the high Tunisian HM herds.

Largest AG and PE variances were found in high HM classes in both populations. The high HM levels were identified as being the most environmentally sensitive among the different contrasted environments. Under unlimited feeding resources and no stressful conditions, a high degree of environmental sensitivity is desired. This postulate can be applied for the case of nearly all the Luxembourg and the high Tunisian HM classes. However, for the other 2 Tunisian environments, a stable production level should be preferred more than a high phenotypic plasticity.

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7.8. References

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Chapter 8

General discussion

H. Hammami

Animal Science Unit, Gembloux Agricultural University, B-5030 Gembloux, Belgium

8.1. Introduction

Sustainable production systems need to be tailored to account for specific physical, social and market conditions. Breeders ought to choose between diversifying their breeding objectives or breeding animals most likely to perform well under a wide range of environments. Nowadays, limited insights about the ability of genotypes to alter their performances in response to varying environments have been achieved. The aim of this chapter is to discuss the main results obtained in the field of G x E using two countries as model, and to focus on the implications of occurring G x E for animal breeding strategies, especially for Luxembourg and Tunisia Holstein populations breeding programs. Furthermore, discussion will be extended to deal with sustainable dairy system development.

8.2. Magnitude of Genotype by environment interaction for milk yield in dairy cattle

The genealogical analysis presented in Chapter 3 illustrates the effects of the extensive use of AI and highlights building up genetic links and relatedness between geographically distant Luxembourg and Tunisian Holstein populations that rely on semen imports. High yielding aptitude of Holsteins supported the widespread use of this breed all over the world. The flow of genes of few selected highly related sires by internationally operating breeding organizations led to high genetic relationships within and across Luxembourg and Tunisian, and also among other cattle populations. The Holstein genes were intensively introduced into these two and other major populations in the world. Therefore, results from Chapter 3 can be extrapolated to other Holstein populations all over the world.

However, results presented in Chapter 4 showed that milk production of Holstein cows under the Tunisian conditions was low to moderate; suspecting difficulties of high-producing cows to express their potential under limited production circumstances. Genetic parameter estimates obtained for milk traits in the Tunisian population were low compared to most estimates reported on large Holstein populations in the northern hemisphere. However, the Tunisian estimates were still in the same range of estimates found in other low- to medium-input systems.

Genetic similarities between Luxembourg and Tunisian Holstein populations were ascertained in Chapter 3; therefore both populations were studied together. Genetic parameter estimates of milk traits were thus compared between both populations firstly using the fact that these two populations have genetic links through the use of common sires (Chapter 5) and secondly using extended genetic relationships among all animals (Chapter 6). Parameter estimates of Luxembourg Holsteins differed significantly from the Tunisian ones. When a random regression TD sire model was applied, using the country border delimitation as a separate trait, heritability estimates of 305-d milk yield and persistency were 73 and 78% lower in Tunisia compared to than those values found in Luxembourg (Chapter 5). The low heritabilities for the Tunisian Holstein population could be explained by reduced sire variances and increased cow environmental effect signaling that stressful conditions including limited feeding resources, poor management and heat impede daughters of imported sires to express their genetic potential under harsh environments. The applied sire model has the advantage of increasing information per sire which could be somehow appropriate for the data structure in our study. However, this model ignores all the relationships between cows and assumes that mating is random, which may result in an underestimation of additive genetic variances. In fact, Tunisia imported many heifers from Germany and the Netherlands, where almost half of the Luxembourg ancestors originate from the same two countries (Chapter 3). Thus, ignoring relationships among cows in Luxembourg and Tunisia may lead to bias in genetic parameters estimation. Being aware of the sire model limitations (partial use of the information, resulting by simply using sires' relationships), another investigation (Chapter 6) was conducted where genetic parameters of yield traits between Luxembourg and Tunisian populations were compared using a test-day random regression animal model. Results obtained by the latter model confirmed differences found between the two populations. Genetic parameters of lactation curves revealed a differentiated gene expression in favor of high-input systems in Luxembourg. A high heritability for 305-d milk yield and a moderate one for persistency found in Luxembourg Holsteins give more possibilities for effective selection to generate genetic progress under their producing environments in comparison to the Tunisian conditions. However, heritability estimates of milk traits obtained with the animal model were higher than those obtained with the sire model for both countries, most likely because maternal contributions were accounted for using the whole pedigree information. Furthermore, the animal model has the advantage of correcting for non random mating of sires, which is most likely the case as in both countries used sires are already proven.

The first investigation of G x E was based on character state models where milk yields in Luxembourg and Tunisia were considered as separate traits and where each country was fitted as a distinct environment: a high input-system for Luxembourg and a low- to medium-input system for Tunisia. Effects of G x E were estimated for milk yield and persistency using random regression TD models (Chapters 5 and 6). Significant G x E was detected for milk yield and persistency. Large differences in genetic and permanent environmental variances between the two countries were observed. Genetic correlations between yield traits in Luxembourg and Tunisia were as low as 0.50 for 305-d milk yield and 0.43 for persistency, when estimated by the random regression TD sire model (Chapter 5). Correspondent values using the animal model (Chapter 6) were 0.60 and 0.36, respectively. Moreover rank correlations and regression coefficients obtained among EBV of sires for milk yield from within Luxembourg and Tunisia analyses were lower than those found by the joint analysis. These low correlations reflect a high re-ranking of common sires between the two environments. Genetic correlations found in this study were lower than almost all those found by within- and across-country investigations cited in the literature (Chapter 2). However they were still in the same range of estimates reported between Kenya and the United Kingdom environments (Ojango and Pollot, 2002).

A herd management definition reflecting feeding intensity and management care was adapted to cluster herds in each country. Three HM levels were used to investigate the magnitude and effects of G x E within- and across-country environments. Results compiled in Chapter 7 demonstrate that the magnitude of genetic correlations and of the effects of G x E differed across the various environments defined. In Luxembourg, the use of the environment descriptor (herd management) did only depict heterogeneous genetic variances for milk yield with limited re-ranking of sires across the three contrasted environments. In contrary, low genetic and rank correlations among EBV of sires within the Tunisian environments indicate serious re-ranking of sires. Genetic correlations of milk yield across Luxembourg and Tunisian environments were in general below 0.80, the cut off value often proposed as indicative of a biologically important G x E. Nevertheless, genetic correlations for milk yield between medium and low herd management levels in Luxembourg and high HM environments in Tunisia were close to 0.80. Cows in low and medium herd classes in Luxembourg may be considered as a good performance predictor of their half-paternal sisters in the high HM class in Tunisia.

8.3. Genetic improvement programs sustainability in high- and low-input systems

Any sustainable genetic improvement program should consider ongoing practices and strategies in the country (breeding goals and selection criteria) and its capacity for organizing and monitoring the evolution of the breeding sector (data recording, genetic evaluation, selection and genetic progress monitoring). In high input-systems, milk traits have been the main breeding objective for many years, but emphasis on functional and durability traits has increased in last years (Miglior *et al.*, 2005). In low- to medium-input systems as in Tunisia, dairy herds differ significantly with respect to management and production levels and are in general managed (owned) by smallholders with little to no training in genetics. Facing the low performance of autochthonous breeds, exotic high yielding breeds essentially Holsteins were lately and continuously introduced to overcome the local deficit in milk products. Unfortunately, the lack of consistent national genetic evaluation and the absence of strategies to select for adaptive traits among productive traits in different environments may accentuate the G x E effects and consequently may lead to unsustainable breeding programs in different cases over the world.

8.3.1. High-input systems (e.g., Luxembourg)

In Luxembourg, dairy cattle are selected based on a composite index (RZG) applied jointly with the German population. The RZG index includes breeding values for production, functional and reproduction traits weighted by specific economic weights (Interbull, 2007). In this thesis, the high milk yield level and large genetic variances observed in the Luxembourg environment (Chapters 5 and 6) show that there is enough potential for breeders to easily identify superior animals as candidates for selection. Moreover, the most common form of G x E effects obtained between the three HM levels in Luxembourg environments was only a scaling effect resulting from heterogeneous variances across these environments (Chapter 7). Differences in production levels between these environments were proportionate to those observed on HM levels. The low management level represents the low input system in Luxembourg where feeding, equipment and labor costs are reduced which should lead to greater net profit even if milk production is decreased. Genetic correlations among milk traits in the three contrasted environments were high. These results confirm that there was almost no re-ranking of sires in Luxembourg for milk yield. This fact prevents the formation of specific breeding scheme for any of these production systems. However, ignoring heterogeneity of variances could favor animals from environments with larger variances to be selected and may result in a bias in the reliability of EBV (Hill *et al.*, 1983). Thus, pre-adjustment in the data as proposed by Wiggans and VanRaden (1991) or correction in the genetic evaluation model such as reported by Meuwissen *et al.* (1996) could be sufficient to absorb the scaling effect and therefore take into account the G x E effect with no risk of mistakes in choosing genetically superior animals during the selection process on national level. In fact, there is no clear benefit to present a specific-environment list of EBV for milk yield, but it is recommended to adjust for heterogeneity of variances in the national evaluation as is done in the German evaluation which includes data from Luxembourg (Reents *et al.*, 1998). This postulate could be justified given the size of the country and especially the expected added value to gain from considering probably insignificantly different economic weights for milk yield in the different contrasted Luxembourg environments. However, breeding goals susceptible to support G x E effect should take into account not only genetic parameters of the various traits in the selection criteria but also their economic weights in the different environments. Scaling effect without re-ranking observed across environments for specific traits can lead to re-ranking across those same environments when selection operates on a composite merit index (Namkoong, 1985). Therefore, further investigation is needed to estimate genetic parameters and magnitude of G x E for functional and fertility traits across the various environments and to obtain their appropriate economic values in each specific environment. Nevertheless, expected form of G x E for nearly all these traits should be mainly a scaling effect when considering the findings of Calus (2007) in the Dutch dairy population which has a lot of similarities in genetic resources and environmental conditions with the one of Luxembourg. However, economic values across environments are susceptible to be more specific across countries and also within the various production environments in the same countries. If we assume that there is only heterogeneous variances as a G x E effect for all traits across environments but differences in economic values are significant across environments, a correction to absorb the scaling effect and the use of an average economic value across environments could be sufficient to come up with only one composite merit index for all the contrasted environments.

In Luxembourg, as in most high-input production environments, G x E were small because genetic improvement programs are well organized, data recording is efficient, some young bulls have been recently tested, even if this is limited in Luxembourg compared to other countries, and the genetic evaluation is effective. Breeding organizations have the capacity to recreate production conditions in the farm level as closely as possible to the breeding populations from where animals or bulls were imported. Increased productivity in response to HM level in Luxembourg (with a sufficiently appropriate feeding level) allows for selection to be particularly effective. Thus, given the non significant G x E across the different Luxembourg environments observed in this thesis, the choice of whether to select a specific genotype for a particular system (management level) to the evolving genotype would not matter anyway. However, such production systems are susceptible to be challenged because of climate change and feed quality problems. In such cases, feeding and management models actually applied for grazing and pasture-based dairy herds may require adaptation in order to be optimal for higher genetic merit animals knowing that US and Canadian sires are tested under conventional conditions of HM.

The HM environmental parameter used in this thesis was a good surrogate of milk production reflecting variation in yield levels from month to month because of varying management practices and feeding resources that are readily available (Chapter 7). However, combining fine defined environmental descriptors including meteorological indices with variables from milk recording data should be further investigated to predict the animal reaction to predictable changes more reliably.

8.3.2. Low- to medium-input systems (e.g., Tunisia)

Results resumed in Chapters 5, 6, and 7 confirm that significant G x E effects were found for milk yield considering Luxembourg as a high-input system and Tunisia as a low- to medium-input system and where production environment was defined in different ways (country or herd management level). Given the same genetic material shared by these two populations with high genetic relatedness and similarities (Chapter 3), genetic expression was severely hampered under the Tunisian conditions and response to indirect selection was limited. Deep re-ranking of common sires shared by both populations has occurred indicating that animals genetically superior in one environment may be inferior in other environments. Low genetic correlations for milk yield between those two populations (based on a country border definition) and also the presence of re-ranking may question benefits from collaboration programs across environments (high- and low-input systems). A genetic correlation lower than 0.60 as a break-even point for separate breeding schemes, collaboration between breeding programs might not lead to higher genetic gain (Mulder, 2007). However, results resumed in Chapter 7 showed that except for the high managed herds, cows producing in low and medium Luxembourg HM levels could be considered as a good performance predictor of their half-paternal sisters in the high Tunisian managed herds. Information about daughter expression in low management level in a country with dominant high-input production systems may be useful for across-country evaluation and benefic for low-input systems. But, more ideally could be that countries actually not participating in international evaluation (essentially developing countries) should be encouraged to become active members in Interbull. Therefore, their participation allows them to get valuable feed-back about their specific production systems and beneficiate from adequate solutions by selecting sires suitable for their production circumstances.

An alternative would be that at least the Luxembourg environments (medium and low) could be clustered together with the high Tunisian management environment to form a similar system in an international evaluation that takes into account G x E ignoring country borders as proposed by some studies in the field (Weigel *et al.*, 2001; Zwald *et al.*, 2003). Otherwise, given the genetic correlation of 0.62 obtained using Luxembourg and Tunisia as a separate character states, they should be considered as two diverse production systems as it is the case in the current international evaluation.

The high G x E effect found using the two country model shows that the indirect selection is less effective compared to direct selection in the target environment. Moreover, the very small daughter responses in Tunisian environments (especially low) because of clearly reduced genetic expression under the limited conditions indicate that changes to improve breeding schemes are justified. Therefore, breeding objectives should not be focused on high performances of intensively selected animals, but on maintaining a cost effective production levels and also on cultural and social aspects under any of the prescribed environments. The question remains how this can be achieved in the current situation? Tunisia as low- to medium-input system, should equitably balance between well-adapted imported semen and implementing in the near feature a local progeny testing scheme. Importation of semen is justified from a genetic point of view when the genetic correlation between countries is > 0.75 (Goddard, 1992; Mpofu *et al.*, 1993). The choice of breeding schemes could therefore be restricted between straight pure breeding or/and cross-breeding. In low-input systems, adaptation to the production environment is of great importance. In this thesis, good performance and genetic profit were observed in the high Tunisian environment due to available richer feeding resources and better management practices. This group of farms could form an environmental cluster found in temperate regions. Thus, straight-breeding to improve well-adapted exotic breeds may be realistic and selection of bulls and dams taking into account G x E effect from this group could be used to diffuse genetic progress. Cross-breeding with exotic breeds could be a better option than straight-breeding pure breed under Tunisian low management herds, which represent more than 70% of total dairy herds in the country, where limited feed resources and stressors are difficult to improve. Depending on the possibilities to restrict environmental stressor effects, cross-breeding could be opted for by using local and exotic breeds or cross different exotic breeds that are adapted to the local production system e.g. Holstein x Simmental or Holstein x Brown Swiss. Indeed, before opting for each or both of the above breeding schemes, breeding goal, resource requirements and organization should be further discussed. In this thesis, genetic parameters for milk yield traits of Tunisian Holsteins (Chapter 4) showed that heritabilities of milk yield were moderate but still low compared to major estimates in other Holstein populations, especially those found for fat and protein yields. Recording of performance data and pedigree is the main driving force for genetic improvement. Only widely spread and accurate measurements lead to efficient selection. In Tunisia, although the official milk recording system started since the 1960s, only about 10% of the total Holstein population is enrolled in the national recording system in 2000 (Rekik *et al.*, 2003). Even though some new recording methods are being introduced, more efforts should be deployed to extend the system and cover larger number of animals including multi-purpose breeds. More attention has to be paid for data quality. In addition, pedigree depth should be improved as concluded from the genealogical analysis (Chapter 3). The genetic evaluation model identified in this thesis could be implemented to start edition of national EBV of animals and to start incorporating their data in the international evaluation system managed by Interbull. However, research on correction for heterogeneous variances and absorbing G x E effects should be encouraged to improve accuracy of estimated breeding values.

8.4. Dairy system development and competitiveness

Sustainable livestock development should not only involve high production levels to ensure human food security but also efficient utilization, effective management, and conservation of natural resources including livestock, land, and inputs (Fitzhugh, 1993). One of the noble objectives of the sustainable agriculture would be to support creation of farming systems that are able to mitigate or eliminate environmental harms associated with industrial agriculture. A sustainable dairying system should balance between environmental, ethical, social, and economic aspects and ensure animal welfare at short- and long-term visions. When focusing on industrial dairy cattle systems, we can see that during the last 50 years, selection of dairy cows (high yielding breeds e.g. Holsteins) was performed at high management levels in order to cope with market demand. Selection schemes focused on increasing milk yield where conventional agriculture farms relied on nonrenewable resources and consequently led to the erosion of natural resources in accelerated rates that the environment can not cope with. Rations of cows were generally based on fodder cultivated on arable land that could have been used for human food growing (breadstuffs and vegetables). Attempting to get animal products at low costs, disastrous practices were applied that turned cattle (natural herbivores) into carnivores by feeding them meat and bone meals. Those practices resulted in Bovine Spongiform Encephalopathy (BSE) at the beginning of the 20th century. Moreover, intensive use of maize grain and concentrate feeds caused the appearance of the so-called lifestyle diseases and other illness. Furthermore, the use of fertilizer, fuel, and pesticides was a challenging harm for both the environment and human. Long time selection of dairy cattle for milk fat content did lead to large quantities of saturated fatty acids in human milk diets and contributed to chronic diseases particularly cardiovascular disease and some cancers. These facts are sufficient to consider that industrial agriculture systems could lead to unsustainable dairy production systems. Therefore, the attainment of a truly sustainable development should start with and around agriculture because of its ability to provide renewable, plant-derived resources (food, raw materials, energy and oxygen) in more or less self-contained circles. However, new issues such as global climate change, the greenhouse emissions from agriculture, and the competition between food and non-food products (i.e. energy, bio-ethanol) from agriculture biomass are emerging as new truly challenging problems.

This thesis shows that substantial differences exist between Holsteins in terms of their sensitivity to production environment. This implies that animals were differently affected by high-input and low- to medium input systems. The occurrence of interaction between the production systems and genotypes would seriously affect the sustainability of the dairying system. With respect to milk yield, the Holstein-Friesian dairy cows were well suited to the conventional higher input production system in Luxembourg, where constrained feed resources and environmental stress are limited. Several reasons questioning the sustainability of the current production systems should be considered:

1) the selection for increased yield of milk, fat, and protein led to substantial deterioration of fertility and health affecting animal welfare of the international Holstein population (Kuhn *et al.*, 2006). Liu *et al.* (2008) reported a deterioration of fertility and longevity in German, Austrian, and Luxembourg dairy cattle populations. They concluded that including fertility traits in selection indices may reduce negative effects on fertility caused by correlated response from selection for milk yield and therefore improve longevity. **2)** The shortage in farmland, severe environmental standards, high quota prices, and high levels of fixed costs are beginning to affect the efficiency and limit net profit in Luxembourg. Conter (2008) reported that since 2003, most of the profit of Luxembourg dairy farms consists of public aids. **3)** The high energy consumption and the actual CO_2 emissions (30 t/a per head) in Luxembourg rates the country in the first place internationally (Stoll *et al.*, 2008). This fact and given the land availability could put in pressure and in competition the utilization of biomass from agriculture and the preservation of the environment. And **4)** The impact of over-consumption of animal-based diets on human health could be disastrous. Stoll *et al.* (2008) reported that Luxembourg people eat in average 300 kg of animal products per year which is at least twice much as a balanced diet needs. Although these limitations are complex and have no single preset solution, recommendations and proposals to enhance the development of a sustainable dairy sector in Luxembourg will be discussed thereafter. At first, we think that consumers and civil organizations should be more sensitized to reduce consumption of animal products. Moreover, pastureland based feed is favorable for cows to provide healthier products with a convenient ratio of omega-3 to omega-6 fatty acids. Soyeurt *et al.* (2007) confirmed the genetic variability of fat composition and supposed that this variability is sufficient to be considered in an animal selection program. In terms of economic profitability and in order to reduce fixed costs, dairy farmers in Luxembourg should choose between increasing farm sizes, decreasing production costs, or even moving to semi-intensive and extensive production systems and employing grassland based dairy strategy to even see reducing milk production level. Indeed, increasing farm size and production levels requires strong demand for animal feed and seems unrealistic with limited farmland, increased pressure on land and water resources, and increased pollution from manure and chemical products. Thus, this strategy would be unsustainable because it is not able to halt climate change, environmental, social, and economic undesirable side effects. In contrary, reducing herd sizes may limit greenhouse gas emissions effects and more realistic in terms of mitigation of climate changes. By means of pastureland based feeding, cows are able to produce milk with healthier fine components as well as organic manure without being a competitor for the human food chain. Unlike arable crops do not compete for land with vegetable and fruits production. Arable lands should therefore be exclusively used for straightforward foodstuff cultivation with a minimum utilization of pesticides.

The current dairy breed of choice for developing countries, especially in Tunisia is the Holstein-Friesian. There are significant regional differences in topography, land-use (forage and crop production capacity), and climate in Tunisia. Milk fat and protein contents are not taken in consideration for marketed milk price. Only milk with extremely high germ contents are penalized. Phenotypic and genetic parameters for production traits (Chapter 4, 5, and 6; Rekik *et al.*, 2003; Rekik and Ben Gara, 2004; Ben Gara *et al.*, 2006), for longevity (Ajili *et al.*, 2007), and for somatic cell scores and fertility traits

(Rekik *et al.*, 2008) from Tunisian data revealed limited genetic expression of Holsteins under Tunisian conditions. Results from these studies may lead to suspect the breed sustainability under the current strategies, the stressful conditions, and the unsatisfactory overall management with no or little emphasis on health, adaptation, and welfare. In Tunisia, Holsteins are mainly owned by small farmers with little or even no land. Nevertheless, large-scale farms exist and are located in the north of the country. Animals are managed under a wide range of environments and production systems varying from integrated intensive to extensive systems and even a “road side” system.

The competitive advantage of milk production in integrated intensive system where most herds are in the high HM class (Chapter 7) is noticed. These high performances are obtained by rations made of forages and often complemented with important quantities of concentrates and hay purchased from the market. Nevertheless, low fertility and short herd life were reported for this system (Ajili *et al.*, 2007; Rekik *et al.*, 2008) which puts in doubt their economic profit and sustainability. Heat stress, management practices, and feeding possibilities and high fixed costs (for machinery, energy, fuels, labor, and raw materials for concentrates) may reduce viability of such a system with large herd sizes (> 200 cows/herd). By concentrating hundreds to thousands of animals in confined buildings, this production system constitutes a threat to both the environment and human health. It also requires cooling systems to reduce heat stress and expensive automation systems to control reproduction, feeding, milking, etc. In addition to those limitations, the competition in land-use for fodder cultivation, horticulture, cereals, and tree crops become a challenge. These conditions led to high use of concentrates where raw materials are exclusively imported which became an unbearable short term burden following rises in prices of agricultural products worldwide. Moreover, under this production system, the overexploitation of land, the specialization and crop intensification using more irrigated surfaces with fertilizers and chemical products made soil vulnerable to erosion and salinisation affecting the production of biomass, the ecosystem, and the pollution of surface waters and aquifers. Grenon and Batisse (1989) recognized that under the current practices, Mediterranean regions are expected to lose nearly 1% of their land capital each year. The ideal for efficient dairy systems would be to have good relation between requirements of animals (ruminants) and the capacity of the farming system to provide enough forage in harmonic environmental, ethical, social, and economic conditions. The intensification and diversification of forage productions with quota on herd sizes (~ 100 cows) may improve sustainability of these integrated intensive systems. Those units and if redesigned to have low milk output in relation to feed costs, labor, and depreciation under reasonable management skills and acceptable environmental and social conditions could improve reproductive, survival, and adaptative parameters. Maintaining an even year round milk output associated with a year round calving and having cows to be productive in more than 4 lactations from forages and grazing is somehow difficult under Mediterranean climatic conditions. Nevertheless, proposals for the improvement of forages and pasture resources (Kayouli, 2003) were envisaged and should be considered to improve competitiveness and sustainability of Holstein’s production systems.

As most developing countries, milk production in Tunisia is largely based on smallholder family units (more than 70% of farmers have less than 10 dairy cattle), where milk production and income is usually low (DGPA, 2002). The smallholder dairy farming systems are dependent on regional and climatic conditions: a system based on pastures, grazing, and concentrates in the north west mountains and forest clearing regions, a system located in the central east of the country where farmers have nearly no land and where cows are fed exclusively from out-land purchased hay, straw, by-products, and concentrates, and a semi-intensive integrated system with mainly family dairy farms concentrated in irrigated and peri-urban zones known by a disproportionnality between the number of animals and arable area (Kayouli, 2003). Only a few of small herds are enrolled in the national milk recording system. Nearly all those herds are in the low HM class (Chapter 7) where the lowest phenotypic and genetic parameters for production traits were recorded. The most comprehensive surveys and analytical studies on smallholder farms (Kayouli, 2003; Ben Salem *et al.*, 2006; Rekhis *et al.*, 2007; Ben Salem and Khemiri, 2008) corroborate with the results obtained in this study. Those authors stressed the low yields, fertility, and survival performances due essentially to poor nutrition levels, management practices, heat stress, and forages availability. They also pointed out the lack of farmer associations and interest groups among and insisted on the improvement of the degree of involvement of key operators (farmers and their representatives, research, industry). Rekhis *et al.* (2007) conducted a rural appraisal study and came with plausibale proposals if applied they may restraint feeding problem and enhance milk production. Nevertheless, to ensure a sustainable production in smallholder farms, efficiency of dairy cows need to be redefined with respect to valorizing scarce resources, their adaptability to stressful conditions, and their survival under the use of limited capital, labor, and health services, as well as capacity to valorize non-marked benefits. Heat stress is becoming a major restraining factor in the extensive and « landless » production systems and is affecting the smallholder profitability. Local or cross bred cows may replace Holsteins under these harsh conditions. When this strategy was applied to small ruminants, the decline in the size of Tunisian native dairy sheep (Sicilo-Sarde) population (Djemali *et al.*, 2008) was stopped and the livelihood of smallholder dairy sheep was improved. Djemali *et al.* (2008) concluded also that farmers of the native meat sheep were inspired from the Sicilo-Sarde story to promote their breed. A similar case of success can be made for local cattle and their crossbreds with the Brown Swiss breed in the 1970s at the North West region of Tunisia (Sejnane).

Overall, this thesis confirms the existence of G x E for milk yield between the two countries reflecting high-input (Luxembourg) and low- to medium-input systems (Tunisia). It can be concluded from this study that the magnitude of G x E varied from only scaling effects resulting from heterogeneous variances in high-input systems to considerable re-ranking of common sires under limited feeding resources, low management care, and stressful conditions in low-input systems. Impact of G x E on breeding programs should be easy to manage in high-input systems because of their ability to use state of art techniques for genetic improvement and to vary their breeding programs according to the characteristics and needs of the different breeds. Nevertheless, harmful effects of intensive and industrialized dairy systems should be considered. More emphasis should be put on the appropriate selection of breeds under less intensive production systems respecting the ruminant's specificities, allowing preservation of environment and animal welfare. This should also concern the low- to medium-input systems but specifically coherent genetic improvement is a challenge to overcome hard G x E effects for those systems. Selection for adaptive traits among economically valuable traits under their specific conditions is needed. In addition, more emphasis on the improvement of management conditions and husbandry practices for the characteristics of introduced breeds should be undertaken. Under harsh environmental conditions, specific strategies should be dressed to guarantee sustainability in the prevailing production systems with long-term interests (e.g., preserving environment, biodiversity, and rural communities) rather than interests on profit in short-term period. Under global climatic changes, smallholders will resort a great risk. Thus, balancing genotypes and production systems must be a « large battle field » and requires the utilization of diverse genetic resources with appropriate genetic potentials for milk production, adaptation, and resistance to heat stress, and diseases.

8.5. Perspectives and Priorities for the Futur

Results obtained in this study highlight the magnitude and effects of G x E for milk yield from using two importing Holstein populations. The perspectives for their valorization on genetic management and environmental sensitivity fields are to be discussed for the national and international level.

One of the priorities in Tunisia is to start estimating breeding values in a near future potentially using result (e.g., variance components) estimated in this thesis. But, additional investigations on data quality (especially fat) and correction for heterogeneity of variances are further needed before initializing national genetic evaluation chain and integrating the international genetic evaluation. Based on the current situation marked by an unstable sufficiency on milk products, and given the moderate to low heritabilities for milk yield traits found in this thesis, selection emphasis on milk yield traits should be favored in short time. However, selection for improving milk yield traits will have some negative effect on fertility and longevity traits. Therefore, research on genetic evaluation model including production traits, fertility, longevity, tolerance to heat stress is a priority. In addition, investigation of the magnitude of G x E for several durability traits (fertility, longevity, health) when data are available are also needed. Single trait selection is not appropriate because genotypes may become unbalanced during periods of environmental instability. However, multiple trait selection goals clearly defined should keep genetic combinations in balance during the selection process (Blackburn and Cartwright, 1987). The appropriate evaluation model may be a multi-trait and/or a reaction model that accounts for differences among herds in Tunisia. Reaction norms provide the opportunity to estimate genetic parameters for an infinite number of environments. Heat stress and continuous environment descriptors should be more appropriate and advantaged to be analyzed with a reaction norm model-multiple trait analysis including production, fertility, and longevity traits.

In addition to genetic evaluation and in order to restrict negative management and environmental effects, development of tools for predicting production and preventing breeders about management disturbances in short time is recommended. A web application for example could be developed to identify problems observed and give possible recommendations to solve them after each test-day. Given, the information technology and communication development in the country and when some encouragements and facilities for breeder's organizations are deployed, users could be able to save the results to their own farm computer and could also be able to record information needed for national breeding organization.

In this thesis, G x E effects for milk yield were found limited in Luxembourg. However, growing importance given to factors such as animal welfare, environmental protection, distinctive product qualities and human heath should be taken in account. Thus, investigations of G x E on fertility, behavioral, efficiency and feed utilization, and robustness are necessary. Moreover, in spite of climatic changes and usage of more biological techniques, more emphasis on resistance or tolerance to heat stress or to particular diseases is asked. Regarding some economic and animal welfare limitations, high expectations are placed on genomics in the near future for studying these aspects.

The transition from a dairy system to another (i.e. from confinement farms to grazing, pastures-based and even organic herds) raises more difficulties for the selection of the convenient sires in the importing countries. Select tested dairy sires in countries having similarities with the desired production and management circumstances (e.g. graziers from New Zealand or Ireland, or intensive from USA or Canada) is not so ideal, because of the G x E effects, but also because of the limited tested sires in some specific countries (New Zealand, Ireland). Therefore, it should be more realistic for importing countries to select animals in their area for feed efficiency and ability to digest proposed feed diets without altering productive and functional traits under the given environmental conditions. Studies on genetics of feed consumption, feed intake, and energy balance under different environments need to be further investigated.

In this thesis, G x E analysis was based on character states models and testing if genetic correlations between separate traits in different environments are less than one. This approach should be sufficient when considering the size of both countries studied. However more knowledge and exploration of reaction norms models is needed to study the shape of variation of environmental sensitivity depending on more defined environmental variables (temperature, feeding levels, rations, feed intake,…etc). An index combining the most environmental factors should favor such reaction norms models. Nevertheless, important aspects related to the availability and to the procedures of recording these descriptors with a valuable accuracy should be discussed.

Based on the results obtained and their implications on the sustainability of breeding programs, more studies are encouraged to be undertaken between countries or regions sharing some similar production and environmental conditions in the south (e.g. North African countries) or between north and south (northern and southern Mediterranean countries). If those studies are possible, robust protocols for breed comparison should be appreciated to guide international dairy community for efficient and sustainable dairy genetic resources. The procedure to incorporate foreign evaluations and collaboration in this field between countries and Interbull should be made efficient for genetic evaluations of animal populations in other environments.

8.6. References

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List of Publications, Oral Presentations and Posters

1. Publications

Hammami, H., C. Croquet, J. Stoll, B. Rekik, and N. Gengler. 2007. Genetic diversity and joint-pedigree analysis of two importing Holstein populations. J. Dairy Sci. 90:3530-3541.

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2. Oral presentations

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3. Posters

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