Consequences of genetic selection for increased milk production in seasonal pasture based systems of milk production

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Abstract

The data presented in this review show that past selection for increased milk production in Ireland over a 14-year period (1990 to 2003) resulted in increases in milk production per cow but has been accompanied by undesirable side effects in reproduction and survival. Economic analysis in a EU milk quota scenario over this period showed that only 41% of the potential improvement in farm profit was achieved because of impaired reproductive performance. Strain comparison studies show that genetic selection for increased proportion of North American Holstein Friesian genes simultaneous with increased phenotypic milk production was associated with increased milk production per cow, lower body condition score, greater milk production response to concentrate supplementation at pasture and reduced fertility and survival. The lower reproductive performance observed with cows selected for solely high milk production was associated with lower energy balance in early lactation, greater partitioning of additional nutrients towards milk production, inability to achieve desired grass intake from pasture and decreased plasma glucose and insulin growth like factor-1 concentrations. The results suggest that germplasm selected in the future should be from within the management system in which it is to be used, and based on a selection index that combines production and other traits of economic importance.

Keywords: (pasture, genotype by environment, dairy, genetics, strain)

1. Introduction

The EU Common Agricultural Policy set up in 1957 aimed to guarantee food security at stable and reasonable prices to producers by maximising production and protecting agriculture (Whetstone, 1999). The continued reform of the Common Agricultural Policy (CAP), the desire to make production more market focused and the obligation to tailor EU agricultural policy in a way to allow future WTO agriculture negotiations, all suggest a more unstable and unpredictable time ahead. The potential for dairy farmers to secure higher prices for their output to compensate for their increasing costs and downward pressure on product prices as a result of policies at EU level is very limited. Compliance with EU Directives on the environment and food safety (i.e., Nitrogen Vulnerable Zones, Water Framework and Strategic Environmental Assessment) and with International Agreements (i.e., Kyoto Protocol and Gothenburg Protocol) will be required. Farming systems need to be sustainable in terms of the environment and animal welfare. Hence, there is considerable interest in finding new ways of reducing costs and increasing efficiency at farm level. One of the strategies that may be adopted by some European dairy farmers is to develop a lower input pastoral dairy system that would be more environmentally and animal welfare sustainable, have lower fixed costs and be labour efficient.

In broad terms, the breeding goal of most dairy farmers is to increase the profitability of their system of milk production. Most producers and breeders would add that this should be achieved without detriment to animal health and welfare and the environment. While there may be broad agreement on this aim, there is far less agreement on what the main components of profitability are, and how to improve them most efficiently. Compared to a high input concentrate system, returns from milk production will be of similar importance in a lower input pastoral based system, but calf and cull cow sales will be relatively more important. In terms of costs, fixed and variable cost associated with concentrate supplementation are much greater in high input systems, while in lower input pastoral systems, forage costs and costs associated with AI/breeding, veterinary and medicine will be more important. Pasture based systems are capable of low cost milk production with very high milk output per hectare (Penno et al., 1996). In contrast, milk production based on crop products are higher cost but are able to support higher per cow milk output than pasture systems. A feature on all grass-based systems is the limited flexibility to rapidly increase milk production as milk price increases. However, increased production costs will be inevitable when farmers move to maximise profitability when milk prices are high and/or concentrate costs are low.

Until recently milk yield has been the main objective criterion for selection in most temperate countries (Miglior, 2004). Although yield is clearly a major component of profitability, the emphasis it has received is also due to the ease of measurement compared to some other components of profitability. Continued selection for higher milk yield has been questioned on a number of counts. Selection for milk yield has been widely associated with deleterious effects on health, fertility and welfare of cows (for review, see Pryce and Veerkamp, 2001). Secondly, EU policy of a continuation of milk quotas until at least 2015, while at the same time reduced milk prices will require dairy farmers to adapt lower cost systems of milk production. Thirdly, is the trend in milk payment schemes for increased emphasis on milk composition, especially milk protein. Finally, compliance with EU legislation on environment, food safety and animal welfare will necessitate a production system that is more ‘natural’ and ‘welfare friendly’.

Optimal financial performance generally comes from high milk solids yield while maintaining a 365-day calving interval and an involuntary culling rate of less than 10%. Annual total culling rates should be kept at close to 18% to maximise the benefit of age and genetic improvement (Esslemont, 1993; Peters and Ball, 1994). Reduced reproductive performance can have a significant effect on the profitability of a dairy herd (Britt 1985, Dijkhuizen et al, 1985). The effect of longer calving intervals in seasonal calving systems are manifested in terms of lower annual milk yield, fewer calves sold per year, increased costs through longer dry period and reduced profit associated with a slip from a more profitable month of calving to one less profitable. Other increased costs associated with increased calving interval are more services and extra veterinary treatments. It is hypothesised that the relative importance of fertility is higher in seasonal pasture based systems of milk production where breeding and calving are restricted to a very limited time period of the year (Veerkamp et al., 2002).

The long running debate on the importance of genotype by environment interaction has been refuelled by the massive importation of North American Holstein genetics into Europe over recent decades. Until recently most experimental results have indicated little or no importance of breed or strain by feeding system interaction in temperate dairying systems (Holmes, 1995). The greater the genetic diversity among breeds or strains and the larger the differences between the environments in which they are compared, the greater the likelihood of genotype by environment interactions existing (Falconer, 1989). The use of high levels of concentrate supplementation at pasture with animals of higher genetic potential for milk production could reduce the overall profitability of production relative to a grass only system with cows of lower genetic milk yield potential.

The aim of this paper was to examine the implication of increased genetic merit for milk production in pasture-based systems and to review the evidence to the existence of genotype by environment interactions across a range of study types.

2. Implications of increased genetic merit for milk production

2.1. Milk production

Figure 1 shows the trends in phenotypic milk production for milk-recorded cows in the United States, The Netherlands, New Zealand and Ireland since 1985. The rate of increase in milk production per cow per year since 1985 has been 193, 131, 35 and 46kg for the United States, The Netherlands, New

Zealand and Ireland, respectively. This is equilivent to an increase of almost 2% of mean production per annum in the United States and Netherlands while approximately 1% of mean production in New Zealand and Ireland. However, the rate of increase over the last five years has been 72, 70, 136, and 142 kg per cow for the United States, The Netherlands, New Zealand, and Ireland, respectively. The reduction in the rate of increase in milk production per cow in the United States and The Netherlands, and the greater rate of increase in Ireland and New Zealand reflects differences in the rate of change in genetic improvement for milk production and the better economic condition for milk production in New Zealand and Ireland compared to the United States and The Netherlands. It may also suggest that in the US and The Netherlands that ration formulation for dairy cows has not been refined adequately in recent years to take advantage of increased genetic merit

2.2. Body condition score and live weight

Successfully manipulating body condition score (BCS) is acknowledged by most animal scientists as an important management factor influencing milk production, animal health, and reproduction in the modern dairy cow (Domecq et al., 1997; Stockdale, 2001; Buckley et al., 2003). Traditionally, the period of most concern was at calving, although the effects of BCS at breeding and the loss between parturition and the start of breeding on subsequent reproduction have gained considerable attention in recent years (Butler and Smith, 1989; Buckley et al., 2003). The continued increase in genetic merit for milk production has resulted in dairy cows that are under increasing nutritional stress, especially in early lactation. With selection on milk yield only, the correlated increase in feed intake is not large enough to cover the increased energy requirements (Van Arendonk et al., 1991). This implies that selection on milk yield alone is expected to increase the mobilisation of body reserves in early lactation, the magnitude and duration of which is related to reduced health and fertility (Villa-Goodoy et al., 1988; Butler and Smith, 1989; Buckley et al., 2003).

Table 1 shows the BCS (scale 1-5) at calving, first service, nadir and end of lactation for cows from controlled experiments at Moorepark Research Centre, Ireland (Buckley et al., 2000; Kennedy et al., 2003a; Horan et al., 2004b). The data shows that increased selection for milk production (while at the same time increased proportion Holstein Friesian genes) resulted in cows with lower BCS at calving, at first service, at nadir and at the end of lactation; greater BCS loss in early lactation and lower condition score gain from first service to the end of lactation were also evident. The results also indicate that nadir condition score is reached at a later stage of lactation for cows of increased genetic merit for milk production. Veerkamp and Brotherstone (1997) observed similar difference between genotypes and concluded it was the result of increased selection for milk yield, increased proportion of Holstein Friesian genes and increased angularity.

Berry et al. (2003a) showed that the genetic correlation between BCS and fertility traits are all-favourable. The data indicated that cows with a superior genetic merit for BCS had shorter interval to first service, required fewer services per cow and had higher pregnancy rates. Based on the estimated genetic parameters an increase in genetic merit for body condition score of one unit would reduce the genetic merit for calving to first service interval by 3 days, reduce the number of services by 0.32, increase the pregnancy rate to first service by 8 percentage units. Estimated genetic correlation between live weight and fertility traits indicated that although cows of greater live weight had a shorter interval to first service, they required more services and had reduced pregnancy rates.

2.3 Feed intake and energy balance

Strong evidence exists demonstrating that milk yield, feed intake and energy balance are heritable traits, and that selection for a higher yield alone increases feed intake, in addition to a simultaneous widening of the energy gap between yield and intake (for review see Veerkamp, 1998; Veerkamp and Koenen, 1999). Estimated genetic correlations between milk yield and dry matter intake ranges from

0.44 to 0.65 when animals are not fed according to production (Veerkamp et al., 2003). This indicates that the correlated response in feed intake under normal conditions is only half of the extra energy required for the increased milk yield. Hence, the other half of the yield driven energy requirement progressively decreases energy balance with increasing genetic selection for yield, and this energy gap is most likely filled by greater mobilisation of the animals fat reserves. Experiments that compared high and low genetic merit cows for milk production have associated higher genetic merit with greater negative energy balance in both high concentrate indoor systems (Gordon et al., 1995; Veerkamp et al., 1995; Oldenbroek et al., 1997) and pasture based systems (Buckley et al., 2000; Horan et al., 2004b). The results also indicate that the extra loss in BCS that is associated with the increased energy deficit in high genetic merit cows is not compensated when these animals are supplemented with higher levels of concentrate in early lactation. The high genetic merit animal puts the extra energy attained in early lactation from a concentrate-based diet into milk production rather than reducing the energy gap. This suggests that the increased energy gap in early lactation with high genetic merit dairy cows is a result of genetically controlled energy partitioning as well as a consequence of feed intake not keeping up with yield. These physiological processes associated with genetically induced negative energy balance might be different from, or the same as, those associated with underfeeding.

Table 2 shows the effect of genetic merit for milk production on milk production responses to concentrate supplementation and the substitution rate of concentrate for grazed herbage from experiments at Moorepark (Buckley et al., 2000; Kennedy et al., 2003b; Horan et al., 2004c and 2004d). The data shows that increased selection for milk production (while at the same time increased proportion of Holstein Friesian genes) resulted in cows with a higher milk production response to concentrate supplementation at pasture, while at the same time a lower substitution rate (decrease in grass intake per unit of concentrate feed). These milk production responses are much larger (especially for the high merit cows) than most of those published previously, but were similar to those in recent publications (Reis and Combs, 2000; Delaby et al., 2001).

2.4 Metabolites, metabolic hormones and detailed fertility parameters

Glucose and non-esterfied fatty acids (NEFA) are the metabolites that appear to be most affected by selection for higher milk production. Negative energy balance is associated with decreased concentration of glucose and increased concentration of NEFA (Spicer et al., 1990; Lucy et al., 1992). Plasma concentrations of glucose were significantly lower in cows of higher genetic merit for milk production than in cows of lower genetic merit (Snijders et al., 2001; Kennedy et al., 2003a).

High genetic merit dairy cows have higher concentrations of growth hormone (GH) and prolactin, and lower concentrations of insulin than lower genetic merit dairy cows (Hart et al., 1978). Concentration of GH increases rapidly as parturition approaches, and it is one of the several periparturient hormones that facilitates increased body tissue mobilisation (Lucy and Crooker, 2001). The physiological action of GH is initiated when GH binds to growth hormone receptors (GHR) on target cells. The greatest concentration of GHR is found in the liver and adipose tissue (Lucy and Crooker, 2001). The most widely known response to GH is the secretion of insulin-like growth factor-1 (IGF-1) from the liver. Insulin-like growth factor-1 controls the production of GH through a negative feedback process. This is an important mechanism as it defines when body tissue mobilisation ceases. The production of IGF-1 in the liver is nutrition dependent, with reduced production when cows are in low or negative energy balance (McGuire et al., 1995). In this situation, GH production increases, adipose tissue sensitivity to insulin decreases and body tissue is mobilised. When cows achieve a more positive energy balance, GH binds to growth hormone receptor-1A (GHR-1A) in the liver and a series of processes result in increased IGF-1 production. Increased concentration of IGF-1 in blood, provides a negative feedback signal to the pituitary gland to reduce GH production, and thereby reduces or stops the rate of adipose mobilisation. Snijders et al. (2001) showed that on a grass based diet the plasma concentration of IGF-1 was significantly lower in high genetic merit dairy cows in weeks 2 to 10 postpartum than lower genetic merit dairy cows. Lucy and Verkerk (personal communication) have shown that over the last 30 years in New Zealand genetic selection has resulted in a cow with increased plasma concentration of GH and reduced IGF-1 in early lactation in pasture based systems.

Some studies suggest that post-partum ovarian function, as measured by post-partum intervals to ovulation do not differ with genetic merit for milk yield (Harrison et al., 1990; Westwood et al., 2000), while others indicate differences (Jonsson et al., 1999). Horan et al. (2004a) showed that strain of Holstein-Friesian did not influence the interval to commencement or subsequent pattern of ovarian activity. The results also show that very early ovulation post partum (commencement of luteal activity <21 days) is associated with a prolonged calving to conception interval and that postpartum progesterone profiles did not differ between cows pregnant and not pregnant to first service.

2.5. Reproduction and survival

Surveys carried out in Ireland in the 1960's and 70's (Crowley et al., 1967; Cunningham et al., 1978; Roche et al., 1978) illustrated that calving rates to first service were high and that culling rates for infertility were low; over 60% and less than 10%, respectively. Calving intervals of less than 365 days were readily observed. A review of herds participating in the Dairy Management Information System (DairyMIS) run by Teagasc Moorepark (Crosse, 1991) showed that calving rate to first service fell over the period 1991 to 1996, from 53% to 49% (O'Farrell and Crilly 2001). More recently, Evans et al. (2002) reported a pregnancy rate to first service of 48% for 74 spring calving herds in both 1999 and 2000 calving season. Similarly, in Northern Ireland, Mayne et al. (2002) have shown that infertility is a major problem with overall conception rates of 37% to first service. Mee (2004) proposed that the phenotypic decline in fertility in Irish dairy herds was as result of both genetic and environmental factors and their interactions.

Trends in milk production, reproductive performance, and survival were monitored on 5580 Holstein-Friesian dairy cows on 14 Irish seasonal calving dairy farms between 1990 and 2001 (Evans et al., 2004a). Over this period calving rate to first service reduced by 0.96% per year (i.e., 55% to 44%), calving rate to first and second service reduced by 0.84% per year (i.e., 77% to 70%) and parity number reduced by 0.10 lactations per year (i.e., 4.3 to 3.5). At the same time number of inseminations per conception increased by 0.02 per year (i.e., 1.54 to 1.75), while calving to conception interval remained unchanged. Over the same period, the proportion of North American Holstein Friesian (NAHF) genes in the cows increased by 5.5% per year (i.e., 8% to 63%), while predicted differences for milk yield (PDMILK) of the cows increased by 25 kg per year. Simultaneously, the predicted difference of the sires of the cows for calving interval and survival increased by 0.5 days and reduced by -0.12% per year respectively. There was a significant negative association between the likelihood of calving rate to first service and calving rate to first and second service with increased PDMILK. Both increased proportion of NAHF genes and PDMILK had a significant effect on survival; increasing the proportion of NAHF from 0 to 100% increased the hazard ratio or risk of culling by 1.77, while increasing PDMILK by 500 kg increased the risk by 1.43. These results are similar to the overwhelming evidence that increasing genetic merit for milk yield reduces fertility and survival (for review, see Pryce and Veerkamp, 2001).

Table 3 shows the reproductive performance of alternative strains of dairy cows from controlled experiments at Moorepark (Snijders et al., 2001; Kennedy et al., 2003a; Horan et al., 2004b). The data shows that increased selection for milk production (simultaneous with increased proportion of Holstein Friesian genes) resulted in cows with lower reproductive performance in terms of pregnancy rate to first service, six week in calf rate, number of services per cow and overall pregnancy rate at the end of a 13-week breeding season

The highest pregnancy rate to first service, six-week incalf rate and overall pregnancy rate was achieved with the New Zealand Holstein Friesian strain. The results also show that the increased selection for milk production (while at the same time increased proportion Holstein Friesian genes) was accompanied genetically by cows with increased calving interval and reduced survival.

Using the data set in Table 3 from all three studies (Snijders et al., 2001; Kennedy et al., 2003a; Horan et al., 2004b), Table 4 shows the reproductive performance, BCS and milk production by quintile for predicted difference for calving interval. The results show that cows genetically predisposed to shorter calving interval had significantly better reproductive performance, lower milk production, and higher BCS at first AI and at nadir than cows with the longest calving interval.

2.6. Economic profitability

Reproductive performance affects the amount of milk produced per cow per day of herd life, breeding costs, rate of voluntary and involuntary culling, and the rate of genetic progress for traits of economic importance (Plaizier et al., 1997). In Ireland, the majority of dairy farms are grass-based, seasonal-calving milk production systems (Dillon et al., 1995). The mechanism used to match feed demand to feed supply is to have calving concentrated in spring. To achieve this, there must be a high pregnancy rate within a short time period following the planned start of mating in late April or early May.

Long herd life substantially decreases the replacement costs per lactation and enables a cow to achieve her maximum capacity of performance when attaining full maturity. With improved cow longevity fewer replacements are required, hence higher selection intensity among dam is possible. In addition, the potential for a long herd life resting on good health and fertility reduces treatment costs and the incidence of involuntary culling, which increases the scope for voluntary culling. Lopez-Villalobos et al. (2000) showed a dual effect of increased survival on profitability through lower replacement rates and higher milk yields with higher proportions of mature animals in a simulation study of seasonal calving herds in New Zealand.

It is hypothesised that the relative importance of fertility is higher in Ireland because milk production is based to a large extent on seasonal pasture production systems and thus breeding and calving are restricted to a limited time period of the year (Veerkamp et al., 2002). The milk production, replacement rate and calving pattern of fourteen Irish seasonal calving dairy farms between 1990 and 2003 (Evans et al., 2004a) was included in the Moorepark Dairy System Model using 2003 costs and prices (Shalloo et al., 2004) across each of the fourteen years (Evans et al., 2004b). Two milk production scenarios were investigated which included EU milk quota applied at farm level (S1) and a scenario with no quota restriction (S2). The influence of variation in milk price, cull cow value and replacement heifer cost were modelled using stochastic budgeting. In S1 there was a significant linear increase ($P < 0.05$) in margin per cow (€10.8), margin per kg of milk produced (0.13 cent) and net farm profit (€546) over the 14-year period. Similarly in S2 there was a significant linear increase in margin/cow (€11.3), margin/kg (0.14 cent) and farm profit (€1,089) over the 14-year period. However, the analysis showed that if reproductive performance, calving spread and replacement rate could have been maintained at 1990 levels for each of the 14-years then the increase in profit per cow, per kg of milk and farm per year would have been €22.1, 0.31 cent and €1,341 for S1; €22.8, 0.32 cent and €2,183 for S2 respectively. The results show that only 41% and 50% of the potential improvement in farm profit was obtained in the S1 and S2 scenarios respectively, compared to if reproductive performance, calving spread and replacement rate were maintained at year 1990 levels.

2.6. Dairy cattle breeding

Recently, in Ireland dairy cattle breeding objectives combining milk production, survival and calving interval for pasture-based systems have been established (Veerkamp et al., 2002). The new index differs from the old “RBI index” in that it contains two new traits (survival and calving interval) as well as three milk production traits (milk, protein and fat yield). The economic weightings on the five traits in the new index are as follows:-

EBI (€)= -€0.08* PD milk (kg) + €1.50* PD fat (kg) + €5.22* PD protein (kg)

+ €10.77* PD survival (%) – €7.09* PD calving interval (days)

Therefore, the index indicates that increasing protein yield at farm level will improve profit per lactation by €5.22 / kg produced. Reducing culling percentage by 1% will increase profit by €10.77 per lactation. Likewise, each one-day increase in calving interval will reduce farm profit by €7.09 per lactation. When these weights are standardised, the relative weighting on protein yield is largest (32%) followed by calving interval (22%), survival (18%), milk yield (-17%) and fat yield (12%). Thus, in the EBI index 40% of relative emphasis is on fertility/survival (calving interval and survival), with the remaining 60% on milk production

3. Genotype by environment interactions

Genotype by environment (GxE) interaction is defined as “the phenomenon that performances of different genotypes are not equally affected by different environments” (Falconer, 1952). Genotype by environment interactions may involve either a change in the relative magnitude of variances across different environments (a scaling effect) and/or it may involve genetic correlations between the “same trait” in different environments being significantly less than unity (a re-ranking effect). Possible reasons for the phenomenon of GxE interactions may be that some alleles are only expressed in specific environments or that gene regulation may alter across different environments (Schlichting and Pigliucci, 1995; Via et al., 1995).

The existence of GxE interactions may result in reduced genetic progress in breeding programs where genetic merit is estimated using data that is not an adequate representation of the herd environments where the test sires' daughters are likely to be used. If only a scaling effect exists (i.e., the genetic correlation between environments = 1) then the magnitude of genetic gain will differ. However if re-ranking occurs (i.e., the genetic correlation between environments <1) and is not taken into account in, genetic gain will also be reduced and genetic change will be negative if the genetic correlation between the traits in the two environments is negative. Although genetic correlations less than one indicates GxE interaction Robertson (1959) suggested that only genetic correlations less than 0.80 are of biological importance.

Three main categories of studies investigating the existence of GxE interaction in dairy cattle are available in the literature: 1) controlled experiments (Veerkamp et al., 1994; Jonsson et al., 1999; Buckley et al., 2000; Kennedy et al., 2002; Horan et al., 2004c), 2) within country analysis (Berry et al., 2003a; Calus et al., 2002; Kearney et al., 2004a); and 3) analysis of international data (Weigel et al. 2001; van der Linde and de Jong, 2003). Analysis of controlled experiments allow interpretation of the results relative to the factor under investigation with all other factors kept constant or adjusted for in the model of analysis. However, controlled experiments are very expensive and are therefore often small in size reducing the power of identifying statistically significant interactions. The marginal cost of within country or across country analyses are low (in situations where the data is already being collected for national genetic evaluations), however because the environments under investigation are not controlled, it is difficult to attribute any interaction identified to a single environmental parameter.
Historically, genetic selection in dairy cattle has been within country. However, it has been shown (Lohuis and Dekkers, 1998) that global selection can increase rates of genetic progress in dairy cattle by up to 17% compared to within country selection. Such benefits when coupled with the development of the International Bull Evaluation Service (INTERBULL) in 1983 have increased the transfer of dairy cattle germplasm throughout the world. However, such success has in turn raised new doubts relating to GxE interactions. It is often asked how much of the genetic superiority of the best sires is expressed

in different environments and especially in low input environments compared with high input environments. Generally the ideal cow for lower-input pasture based systems is one that produces moderate levels of high composite milk, with minimal intervention on a somewhat limited energy input. In contrast, the optimal cow on a high input system is that which will produce high milk yield on maximal energy inputs.

Genotype by environment research studies of the past tended to focus mostly on milk production traits; however, the diversification of breeding objectives across the world (Miglior 2004) has prompted researchers (Fredeen et al., 1988; Veerkamp et al., 1994; McGowan et al. 1996; Pryce et al., 1999; Buckley et al., 2000) to test for GxE interactions in ancillary traits. Possible ancillary traits include health (e.g., mastitis, somatic cell count), fertility, conformation, BCS, body weight and many more.

3.1. Controlled experiments

Arguably, one of the most well know studies investigating the existence of GxE interaction in dairy cattle is that of the Langhill Dairy Cattle Research Centre. All cows were Holstein-Friesian and were kept indoors from calving (beginning in early September) to July and offered ad libitum access to total mixed rations (TMRs). The diets were designed to achieve, over a full lactation, proportions (in dry matter) of concentrates, brewers grains and silage of 20:5:75 (Low concentrate; LC) and 45:5:50 (High concentrate; HC). Annual average concentrate intakes were 1.0 ton/cow (LC) and 2.5 ton/cow (HC). The herd comprised two genetic groups: a selection line bred to the sires of the highest genetic merit for fat and protein yield available in the UK since 1973, and a control line bred to sires of average national UK genetic merit for fat and protein yield since 1976. Several scientific articles have been published on the existence or lack thereof GxE interactions for milk production (Veerkamp et al., 1995), BCS (Veerkamp et al., 1994), health and fertility (McGowan et al*.,* 1996; Pryce et al., 1999).

Veerkamp et al. (1994) reported higher milk yields and lower BCS during the first 26 weeks of lactation in selected animals as opposed to control animals on the two different diets. However, the selected line lost more BCS, on average, on the LC diet to compensate for their lower intake than the selected line on the HC diet. Veerkamp et al. (1994) concluded that with a high proportion of forage in the diet the selected line was not capable to ingesting much more than the control line, thereby resulting in smaller differences in performance between genotypes. In contrast the selected line on the HC diet had the cumulative advantage of higher dry matter intakes and greater body tissue mobilisation. Veerkamp et al. (1995) also reported that the regressions of milk yield, protein yield and protein concentrations on pedigree index for fat plus protein yield differed across the two feeding systems used in their study. This result implies that the genetic variance for milk yield is greater in higher input systems. Veerkamp et al. (1994) also reported significantly different regression coefficients of BCS on pedigree index for fat plus protein yield between LC and HC diets. This was interpreted to imply that GxE interactions for BCS might become more important in the future if selection for fat plus protein yield alone continues.

McGowan et al. (1996) showed no significant effect of diet on various reproductive parameters (days to first oestrus, calving interval, number of services per pregnancy) although they showed that heifers fed the high concentrate diet had significantly ($P<0.05$) longer calving intervals than those fed the low concentrate diet. Pryce et al. (1999) using a similar data set failed to report any significant GxE interaction for a range of health (mastitis, metritis, ketosis, retained placenta, milk fever lameness) and fertility traits (oestrus not observed, conception to first service interval, calving interval, days to first heat, days to first service and days open) although the interaction for calving interval did approach statistical significance at the 10% level. Nevertheless, the Langhill study was operated on a TMR diet. In countries like Ireland and New Zealand where grazed grass constitutes the main diet of dairy animals, these results may not hold.

Therefore, over the past decade several studies (Buckley et al., 2000; Kennedy et al., 2002; Horan et al., 2004c) at Moorepark Research Centre, have been undertaken to evaluate alternative genotypes of animals across contrasting grass based systems of milk production. The first of these studies ran from 1995 to 1997 (Buckley et al., 2000) and consisted of two genotypes. High genetic merit animals (**HG**) were imported from Holland and France based on superior genetic merit for milk production. Medium genetic merit animals (**MG**) were the daughter progeny of cows in the Moorepark Research herd mated to sires of medium merit for milk production available in Ireland at that time. Cows were randomly assigned to one of three feeding systems: a high stocking rate (**HS**) system (3.0 cows/ha, 380 kg Nitrogen/ha, c.a. 500 kg concentrate/yr); a high concentrate (**HC**) system (3.0 cows/ha, 380 kg Nitrogen/ha, c.a. 1,000 kg concentrate/yr); and, a third feeding system (**MP**) which had a similar nitrogen application rate and concentrate input as the HS system but cows grazed to a higher post grazing sward height. The aim of the MP feeding system was to allow a greater daily allowance of higher quality grass throughout the grazing season. Results from the study revealed no indication of GxE interactions for milk production, live weight (change), BCS (change), dry matter intake, and a range of blood metabolites. The researchers concluded that the difference between either the genotypes or feeding systems adopted in the study might not have been diverse enough to identify any significant GxE interaction across such a small data set.

In order to evaluate this hypothesis further another controlled study was set up at Moorepark with a greater diversity between feeding systems (Kennedy et al., 2002). A HG and MG group were respectively created from Irish high or medium genetic merit dams mated to respective high or medium genetic merit sires for milk production available in Ireland. Average predicted differences for milk production of the sires of the HG and MG genotypes differed by 195 kg (Kennedy et al., 2003a). Three feeding systems, varying only in concentrate feeding level, were implemented. Average annual concentrate feeding level per cow was 376 kg (**LC**), 810 kg (**MC**) and 1540 kg (**HC**); the MC feeding level represented industry norm for seasonal spring calving herds in Ireland at that time. The mean milk yield response in the HM cows to additional concentrate was 0.89 kg milk/kg concentrate dry matter (DM) going from the LC to MC and 1.01 kg milk/kg concentrate DM going from LC to HC. The corresponding values for the MM cows were 0.66 and 0.74 kg milk/kg concentrate DM, respectively. The significant genotype x feeding system interaction in the regression analysis using the individual cow values suggested that individual cows of very high genetic merit may have the expression of their milk potential compromised by inadequate concentrate feeding in a grass-based system. The milk yield response to increasing concentrate feeding was 0.45, 0.84, 1.46 kg milk/kg concentrate DM for cows with PDMILK of <100, 100 to 200, and 200 to 300 kg, respectively. This implies a significant genetic merit by level of concentrate feeding system interaction (i.e. scaling effect) for milk yield across the feeding systems adopted; similar conclusions were also reported for protein yield. A significant genotype by feeding system interaction for BCS at the end of lactation was also reported demonstrating that high genetic merit cows have lower rates of body tissue repletion from early lactation to the end of lactation, especially in the HC feeding system. There was an average difference, over years two and three, in BCS between feeding systems of 0.07 units in the LC system, while there was a difference of 0.40 in the HC system. The results suggest that the value of increased genetic merit in a low concentrate grass-based system of milk production will be less than in a high concentrate system and that the response to increased concentrate feeding depends on the genotype of the animal. The profitability of feeding higher levels of concentrate in Ireland depends on the milk price: concentrate cost ratio, as well as low quota leasing charges. Other factors, namely the health and reproductive performance of high genetic merit dairy cows and environmental sustainability also need to be considered.

A third study at Moorepark was initiated in 2001 comparing three strains of Holstein-Friesian: high production North American, high durability North American and New Zealand strain (Horan et al., 2004c). The high production North American genotype (**HP**) was created through the mating of the top 50% of cows in the Moorepark research herd (based on pedigree index for milk production) with semen from five North American sires chosen on the basis of their superior pedigree index for milk production. Based on pedigree index for milk production, the bottom 50% of cows in the Moorepark research herd were inseminated with semen from five North American sires chosen on the basis of their superior milk production, fertility and linear (muscularity) traits; this genotype was termed the high durability (**HD**) genotype. The difference in predicted transmitting ability for milk production between the HP and HD was almost identical to that of the previous study by Kennedy et al. (2002). The New Zealand (**NZ**) strain animals were imported as embryos from New Zealand and implanted into thirteen-month-old Holstein-Friesian heifers in Moorepark Research Centre. They were selected using the highest possible genetic merit expressed in the New Zealand genetic evaluation system (Breeding Worth). On average, 87·5% of the NZ strain genes was of New Zealand Holstein Friesian ancestry. The three feeding systems adopted were a high milk output from pasture feeding system (**MP**; stocking rate of 2.47 cows/ha; 300 kg Nitrogen/ha; c.a. 350 kg concentrate/cow/yr), a high concentrate feeding system (**HC**; stocking rate of 2.47 cows/ha; 300 kg Nitrogen/ha; c.a. 1,500 kg concentrate/cow/yr), and a high stocking rate feeding system (**HS**; stocking rate of 2.74 cows/ha; 300 kg Nitrogen/ha; c.a. 350 kg concentrate/cow/yr). There was a significant strain by feeding system interaction (scaling effect) for yield of milk, fat and protein (Figure 2). The milk production response to increased concentrate supplementation (MP vs. HC) was significantly greater in both the HP and HD strains (1.10 kg milk / kg concentrate for HP; 1.00 kg milk / kg concentrate for HD) than the NZ strain (0.55 kg milk / kg concentrate for NZ). The data shows that in a grass-based system, aggressive selection for increased milk production (HP strain) in the NAHF has resulted in an animal with higher milk production, greater response to additional concentrate supplementation but with greater live-weight and BCS loss post-calving. The NZ strain selected on a grass-based system for increased fat and protein yield in a given volume of milk had the lowest milk volume, highest milk composition, poorest response to concentrate, lowest live-weight and highest BCS. The HD strain was intermediate for milk production and composition, had the highest live-weight and was intermediate for BCS. The existence of strong strain by feeding system interactions for milk production demonstrates that the optimum system of milk production will vary with strain of Holstein Friesian.

Other controlled experiments in Australia (Fulkerson et al., 2000) and New Zealand (Kolver et al., 2002) have also reported evidence of scaling effects and re-ranking, respectively between genotypes across environments. Fulkerson et al. (2000) reported a smaller difference in fat and protein yield between low genetic merit animals and high genetic merit animals on low concentrate feeding levels (27 kg) compared to high concentrate feeding levels (51 kg). Kolver et al. (2002) reported a re-ranking of New Zealand and North-American genotypes between grazing and TMR diets. Under grazing conditions New Zealand Holstein-Friesians out-produced NAHF for milk solids while the rankings reversed on the TMR diet. Some of this re-ranking may be attributable to differences in intakes for the two genotypes across the two feeding systems. The New Zealand genotype had higher intakes on the grazed grass-based diet compared to the North American genotypes with the opposite being true on the TMR diet. Such interactions were in spite of the two genotypes having the same genetic merit for profitability as measured by the Breeding worth (Harris et al., 1996) at a feed allowance of 4.5 t dry matter/cow/year.

3.2. Within country analyses

Within country analyses differ from controlled experiments in that the size of the data set is usually larger but the number of factors differing across environments equivalently larger, thereby making it more difficult to attribute any phenomenon identified to a single environmental parameter. Nationally reported genetic evaluations are the best estimate of the animal's (estimated breeding values) or its progeny (predicted transmitting abilities) genetic capability in the average environment of the recorded daughter observations within that country. However, accuracy of national genetic evaluations and thus customer (farmer) confidence in estimated breeding values is dependent on consistent ranking and differential between sires across all environments. This is a bigger obstacle in larger countries with more diverse production environments and climates (e.g., US, Australia) compared to countries with relatively more homogenous production environments (e.g., Ireland, New Zealand).

Berry et al. (2003a) using data from 66 grass based dairy herds across southern Ireland investigated the possible existence of GxE interactions for milk yield, BCS, BCS change, live weight and live weight change across different milk production and nutritional environments. The nutritional environments included annual concentrate feeding level per cow, a measure of grazing severity and silage quality. They reported no significant GxE interaction for milk yield across the range of environments investigated with the exception of the silage quality environment. However, several instances of GxE interactions were evident for both BCS and BCS change traits. These were associated with changes in genetic variance and/or genetic correlations between the "same trait" being significantly different from unity (correlations as low as –0.60 were found between extreme milk production environments for BCS change in early lactation). Berry et al. (2003a) concluded that the lack of significant re-ranking of animals for milk yield across most environments may be due to the buffering capacity of the cow to increase intake and/or mobilise body tissue to meet energy demands for milk production. This was similar to the previous results of Veerkamp et al. (1995) from their controlled experiment. Increased reliance on body tissue mobilisation on low input systems may have deleterious repercussions for fertility because of the favourable genetic correlations between BCS (change) and fertility (Pryce et al., 2001; Berry et al., 2003b).

Boettcher et al. (2003) investigated the possible existence of GxE interactions among Canadian dairy herds that practiced either intensive rotational grazing (herds that grazed grass for at least six months of the year) or conventional systems that relied on stored feed. Despite small differences in milk production between the systems (9,400 kg and 9,947 kg milk yield in the grazing and conventional systems, respectively) they reported a scaling effect for milk yield with the genetic variance being largest in the conventional (higher input) systems. The larger genetic variance in the conventional systems translated into a higher heritability in the conventional herds. However, genetic correlations between traits in the two contrasting environments were all near 0.90. They concluded that the effects of GxE interactions among grazing and conventional management systems were small and that farmers practicing grazing can accurately select on sires based on their national genetic evaluation breeding values.

Kearney et al. (2004a; 2004b) investigated the presence of a GxE interaction in grazing versus confinement systems. Grazing herds were defined as those that utilised grazing for at least six months. The regression coefficients indicated that current sire genetic merit in grazing herds might overestimate the expected daughter differences. Genetic correlations were less than one between sire estimated breeding values from the two environments. However, they concluded that the differences were not large enough to justify separate genetic evaluations for each system.

Kolmodin et al. (2002) used reaction norms to describe the phenotypic plasticity of genotypes in Nordic countries for protein yield and days open across different environments of herd-year average protein yield and days open. Phenotypic plasticity measures the degree of robustness, or lack thereof (i.e., plasticity) of the phenotypic expression of a genotype across environments and is often described using reaction norms as a function of an environmental parameter (Bryant et al., 2004). If different genotypes have significantly different reaction norms, then a GxE interaction exists. Kolmodin et al. (2002) reported higher genetic variances and heritability estimates for protein yield at higher production levels. Similarly, the genetic variance for days open increased as herd average days open and protein production increased; the effect on the genetic variance was lower when protein yield was considered as the environmental parameter. Rank correlations for protein yield predicted offspring performance (Kolmodin et al., 2002) were high between average and higher production environments but declined between average production environments and low protein yield environments. They concluded that GxE interactions (both scaling and re-ranking) were present for protein yield and days open across different herd-year protein yield and days open environments.

Calus and Veerkamp (2003) also used random regression methodology to estimate reaction norms for milk, fat and protein yield of Dutch sires across different environmental parameters. Their results failed to reveal any significant re-ranking among sires; genetic correlations between the 25% and 75% quartiles for each environmental parameter were all greater than 0.95. However, they did report heterogeneity of genetic variances across the different environmental parameters studied. Herds with high protein, high persistency, young age at calving, high BCS, and shorter calving intervals expressed the highest genetic variance for milk, fat and protein yield. Nevertheless, because of a comparable heterogeneity of residual variances across the different environments, no difference in heritabilities across environments was observed. This is in contrast with previous results using random regression methodology (Calus et al., 2002; Kolmodin et al., 2002) although the latter studies assumed homogenous residual variances across environments. Calus and Veerkamp (2003) speculated that a portion of the significant scaling effects observed across some of the environmental parameters might be in part attributable to the association with yield, in that as level of production increases so does the variance. Nevertheless, BCS and calving interval also exhibited changing genetic variances across different environments; correlations between BCS and calving interval with average protein yield were 0.19 and –0.01, respectively.

Calus and Veerkamp (2003) also investigated the effects of scaling for milk production on the ranking of animals for a composite index (INET) derived as:

$(-0.08*EBV_{\text{Milk yield}})+(1*EBV_{\text{Fat yield}})+(6*EBV_{\text{Protein yield}})$

They reported only minimal re-ranking of animals on INET across environments. This is partly due to the comparable scaling effects of the casual traits across the environments and also the strong correlation between the traits within the index. They went on to suggest that if traits with scaling effects independent of those for the milk production traits were included in the index then considerable re-ranking of animals on that index may occur.

3.3. Between country analyses

Although not large, by most across countries comparison studies, the "CANZ" study (Peterson, 1988) is probably the best recognised. Twenty Canadian and twenty New Zealand Holstein sires were mated to cows in twenty New Zealand and ten Canadian herds in a factorial arrangement. Sires were selected from available proven AI sires in the two countries at that time. Investigations of GxE interactions were considered at two levels, a macro level (interactions between genotypes and environment) and a micro level (interactions between sire within genotype and environment). Peterson (1988) reported a significant genotype by environment interaction for production traits. Canadian sires did not rank the same in New Zealand as they did in Canada thus indicating that genetic ability of animals to achieve sufficient energy intakes from an exclusively pasture diet. Charagu and Peterson (1998) reported significant macro (genotype) by environment interactions for first lactation protein yield and composition but for no other production traits including mature live weight. They attributed the significant interactions to the larger difference in protein yield and composition when the daughters were producing in New Zealand but no difference when producing in Canada; the Canadian sired cows produced more protein but of lower concentration in New Zealand compared to the New Zealand sired cows. This therefore implies a macro scaling effect but with no re-ranking between genotypes. Graham et al. (1991) did not find any significant macro re-ranking for BCS change and BW change over the lactation between Canadian and New Zealand-sired heifers milked in both Canada and New Zealand. However, the lack of any significant GxE interaction for the majority of traits observed in this study may be due in part to the effect of heterosis obtained through the mating of Canadian sires with New Zealand dams and vice versa. Heterosis estimates between New Zealand Holstein-Friesian and North-American Holstein Friesians are around 3% (Harris et al., 2001). Such heterosis will mask out to some degree the absolute difference in the resulting progeny.

A Irish study (Cromie et al., 1999) regressed sire INTERBULL estimated breeding values for the US against sire estimated breeding values in Irish high (1,514 kg concentrate/cow/yr) and low (505 kg concentrate/yr) concentrate input herds. Although the genetic correlation between sire estimated breeding values in Ireland and their US INTERBULL equivalents were all greater than 0.85, indicating little re-ranking of sires between US and Ireland, the regression coefficients of 0.52 and 0.32 with the high and low concentrate input herds suggested a large scaling effect. This indicated that US bull proofs over-estimated genetic merit for milk production for Irish pasture-based systems; the overestimation was more pronounced in low concentrate input Irish herds. The genetic correlation between milk yield in both Irish environments was 0.92 suggesting a very close similarity in the genetic background controlling milk yield in both environments. Nevertheless the heritability for milk and protein yield was higher in the herds feeding high levels of concentrates compared to the herds feeding low levels of concentrates.

Currently, INTERBULL use the multiple trait across country evaluation (MACE; Schaeffer, 1994) procedure to estimate an international evaluation for each sire on the scale of each member country based on the performance and number of progeny in each country and the genetic correlations between countries. The correlations between countries are less than unity, implying differences in trait definitions, differences in data collection and analysis procedures between countries and/or the existence of GxE interactions between countries. Weigel et al. (2001) estimated the genetic correlation between milk yield across 17 different countries. Correlations among countries that rely heavily on grazed grass (i.e. Ireland, Australia, New Zealand) were ≥0.91. Correlations among countries featuring high milk production in intensively managed herds (US, Canada, Belgium, The Netherlands, Italy) were also ≥0.91. However, the correlations between the rotational grazing countries and the intensively managed countries ranged from 0.80 to 0.90.

To date INTERBULL does not routinely apply MACE procedures to fertility information. However initial studies (Van der Linde and de Jong, 2003) have reported low (–0.05) genetic correlations between longevity across some countries; the average genetic correlation between countries for direct longevity was 0.60. Nevertheless, such low correlations are partially attributable to the diversity in definition of longevity related traits across the different countries. However, the genetic correlation between longevity in Canadian and the US was 0.93 despite alternative methods of calculating longevity in either country (van der Linde and de Jong, 2003). Similarly, genetic correlations between longevity in the European countries assessed using survival analysis varied from 0.56 to 0.88 (van der Linde and de Jong, 2003). Despite this van der Linde and de Jong (2003) concluded that MACE for longevity traits is feasible.

To date INTERBULL through the use of MACE procedures treats the “same” trait in different countries as separate traits. No account is taken of GxE interactions within country (i.e., cows producing on a 40-cow grazing herd in Vermont are considered to be exposed to the same environmental conditions as cows on a 5000-cow feedlot in Arizona) despite differences in environmental conditions within country being as large as differences in conditions between countries (Hayes et al., 2003). Similarly, data originating from herds in close proximity but on opposite sides of a international borders are treated as different traits despite their usually common climate and systems of production. Recent studies (Weigel and Rekaya, 2000; Zwald et al., 2003) have been published which employ cluster analysis techniques or associated procedures to group herds of similar characteristics together thereby facilitating a borderless genetic evaluation in dairy cattle. Such techniques, if adopted, could increase genetic progress through improved accuracy of genetic evaluations for each management category.

3.4. Implications of genotype by environment interactions

Evidence within the literature from controlled experiments and experiments both within and between countries appear to be in somewhat conflict. Some studies reported no GxE interactions (Buckley et al., 2000), others reported only a scaling effect (Cromie et al., 1999; Calus and Veerkamp, 2003; Kennedy et al., 2002; Horan et al., 2004c) while others also reported re-ranking (Carabano et al., 1989; Cienfuegos-Rivas et al., 1999; Kolver et al., 2002; Berry et al., 2003a). Nevertheless, a trend is appearing which suggests that when genotypes and/or environments are considerably diverse, genotype by environment interactions do exist.

In studies that do report a GxE interaction the most common form is as a scaling effect; several instances of scaling effects have been found for milk production between low or high input production systems across controlled experiments (Kennedy et al., 2002; Horan et al., 2004c), within country analyses (Berry et al., 2003a) and between country analyses (Cienfuegos-Rivas et al., 1999; Boettcher et al., 2003;). The increase in genetic variance observed in some environments is important for animal breeders since there is a greater probability of animals from herds or with relatives in herds expressing larger genetic variance being more easily selected and their estimated breeding values over predicted (Hill, 1984). The increase in genetic variance with higher input systems also has important implications for both feeding and other management decisions. For example, the response to concentrates will differ for high and low genetic merit cows, and, therefore, the same nutritional models cannot be applied across all animals. In other words, the feeding systems developed in the past for animals of lower genetic merit may require adaptation in order to be optimal for higher genetic merit animals. The change in genetic variance across environments also suggest that the return on investment in genetic improvement for some traits may be greater in environments expressing higher genetic variance or that farmers operating in environments with larger genetic variance may be able to pay more for semen than farmers in environments with lower genetic variance.

Nevertheless, the practical implications of scaling may be considered to be lower than the implications of re-ranking. When re-scaling occurs, in the absence of re-ranking, an animal maintains its genetic ranking across environments although the absolute difference in genetic merit compared to other animals may be reduced/increased. Scaling effects can be accounted for in breeding value estimation (Meuwissen et al., 1996) and do not influence the ranking of animals on the trait in question. However, if scaling exists for a range of traits included in a composite index (e.g., a national breeding objective) the relative weighting on the traits within the index may alter thereby possibly leading to re-ranking of animals on the index itself (Namkoong, 1985). Charagu and Peterson (1998) drew attention to the fact that traits like “economic efficiency” which is a composite of other traits may also exhibit such phenomenon. In order to avoid such phenomenon Calus and Veerkamp (2003) suggested the inclusion of environmental plasticity in breeding decisions rather than adjusting for it in the statistical model

In contrast, when re-ranking occurs, animals genetically superior in one environment may be genetically inferior in other environments and may therefore, in theory, result in unfavourable genetic trends if the genetic correlations are negative. Significant re-ranking of individuals for some traits observed in some across country analyses may suggest a possible advantage of separate breeding programs within the different environments. However, the implementation of separate breeding programs within different environments will depend not only on the evidence of re-ranking between the environments but also on the increase in costs of progeny testing in both environments. Therefore the economic benefit of a separate breeding program will be a function of the cost of the breeding program and the expected change in genetic gains achievable over the importation of genetics from another environment. The change in genetic gain between both environments will be a function of the genetic (co)variances between the environments (assuming similar selection intensities and similar accuracies of selection).

4. Conclusions

The data presented in this review show that selection for increased milk production in Ireland over a twelve-year period (1990 to 2001) has resulted in increases in milk production per cow but has been accompanied by undesirable side effects in reproduction and survival. Strain comparison studies showed that selection for increased proportion of North American Holstein Friesian genes while at the same time increased milk production was associated with increased milk production/cow, lower body condition score, greater milk production response to concentrate supplementation at pasture and reduced fertility and survival. Failure to get in calf and maintain a 365-day calving interval was the main reason for the reduced survival within the seasonal dairying system, rather than failure to start cycling after calving. Evidence suggests that these differences in fertility and survival are maintained across different levels of concentrate supplementation. Genotype by environment interactions are evident in situations of diverse genotypes and/or production environments. This suggests that germplasm selected should be from within the management system that it is to be used, using a ‘balanced’ selection index that combines production and other traits of economic importance.

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Table 1. *Comparison between different strains of Holstein-Friesian cows for measures of body condition score*

Study	**Buckley et al. (2000)**		**Kennedy et al. (2002, 2003a)**		**Horan et al. (2004c)**		
Strain[a]	**HM**	**MM**	**HM**	**MM**	**HP**	**HD**	**NZ**
Milk yield (kg)	7,779	6,862	7,841	6,855	6,958	6,584	6,141
Predicted difference milk (kg)	230	-4	156	79	187	76	48
BCS[b] **at calving**	2.73	3.14	3.29	3.41	3.17	3.24	3.37
BCS at first service	2.39	2.97	2.85	3.04	2.78	2.93	3.07
BCS at drying off	2.50	2.96	2.86	3.05	2.68	2.93	3.13
Nadir BCS	2.19	2.70	2.61	2.79	2.45	2.65	2.84
Day in milk of Nadir BCS	160	153	197	182	167	153	146
BCS loss calving to first service	0.35	0.19	0.40	0.33	0.35	0.27	0.27
BCS gain AI to end of lactation	0.09	0.01	-0.02	-0.01	-0.11	-0.02	0.06

a HM = High Genetic Merit, MM = Medium Genetic Merit, HP= High Production, HD = High durability, NZ = New Zealand

b Scale of one to five

Table 2. *Comparison between different strains of Holstein-Friesian cows for measures of milk production responses to concentrate supplementation and substitution rate of concentrate for grazed grass*

Study	Strain[a]	PD milk[b]	Response to supplementation (kg milk/ kg DM conc.)	Substitution rate (kg grass/ kg DM conc.)
Buckley et al., 2000	HM	230	1.12	0.25
	MM	-4	0.92	0.40
Kennedy et al. 2003c	HM	156	1.01	0.36
	MM	79	0.74	0.57
Horan et al. 2004c; 2004d	HP	187	1.10	0.19
	HD	76	1.00	0.35
	NZ	48	0.55	0.51

[a] HM = High Genetic Merit, MM = Medium Genetic Merit, HP= High Production, HD = High durability, NZ = New Zealand

[b] PD milk = Predicted difference for milk yield.

Table 3. *Comparison between different strains of Holstein-Friesian cows for measures of reproductive performance*

Study	**Snijders et al. (2001)**		**Kennedy et al. (2003a)**		**Horan et al. (2004b)**		
Strain[a]	**HM**	**MM**	**HM**	**MM**	**HP**	**HD**	**NZ**
North American HF (%)	92	50	80	60	92	82	15
PD milk (kg)	230	-4	156	79	187	76	48
PD calving interval (days)	1.16	-0.97	0.43	-0.57	0.40	-1.20	-1.59
PD survival (%)	-0.05	0.09	-0.20	-0.03	-0.55	0.41	1.23
Submission rate (%)	88	93	85	90	78	90	88
Pregnancy rate to first service (%)	45	51	49	57	45	54	62
Services per cow (no)	2.1	1.8	1.9	1.8	2.1	1.8	1.6
Six week in calf rate (%)	60	67	63	66	54	65	74
Overall pregnancy rate (%)	82	93	83	88	74	86	93

[a]HM = High Genetic Merit, MM = Medium Genetic Merit, HP= High Production, HD = High durability, NZ = New Zealand

Table 4. *Variation in reproductive performance by quintile for predicted difference for calving interval*

Quintile	**Q1**	**Q2**	**Q3**	**Q4**	**Q5**	**Sig.**
PD calving interval (days)	**2.17**	**0.59**	**-0.50**	**-1.18**	**-2.09**	
PD survival (%)	-0.85	-0.14	0.14	0.34	0.99	
PD milk (kg)	233	179	82	69	51	
Pregnancy rate to first service (%)	44^{a}	46^{a}	56^{b}	57^{b}	58^{b}	**
Services per cow (no)	2.03^{a}	1.91^{ab}	1.82^{b}	1.67^{c}	1.74^{bc}	**
Six week in calf rate (%)	57^{a}	57^{a}	70^{b}	69^{b}	68^{b}	**
Overall pregnancy rate (%)	80^{a}	81^{a}	86^{ab}	91^{b}	91^{b}	**
Milk production (kg/cow)	6811^{a}	6965^{a}	6556^{ab}	6417^{bc}	6254^{c}	***
BCS at first service	2.65^{a}	2.75^{b}	2.94^{c}	2.98^{cd}	3.03^{d}	***
Nadir BCS	2.39^{a}	2.46^{a}	2.64^{b}	2.69^{b}	2.79^{c}	***

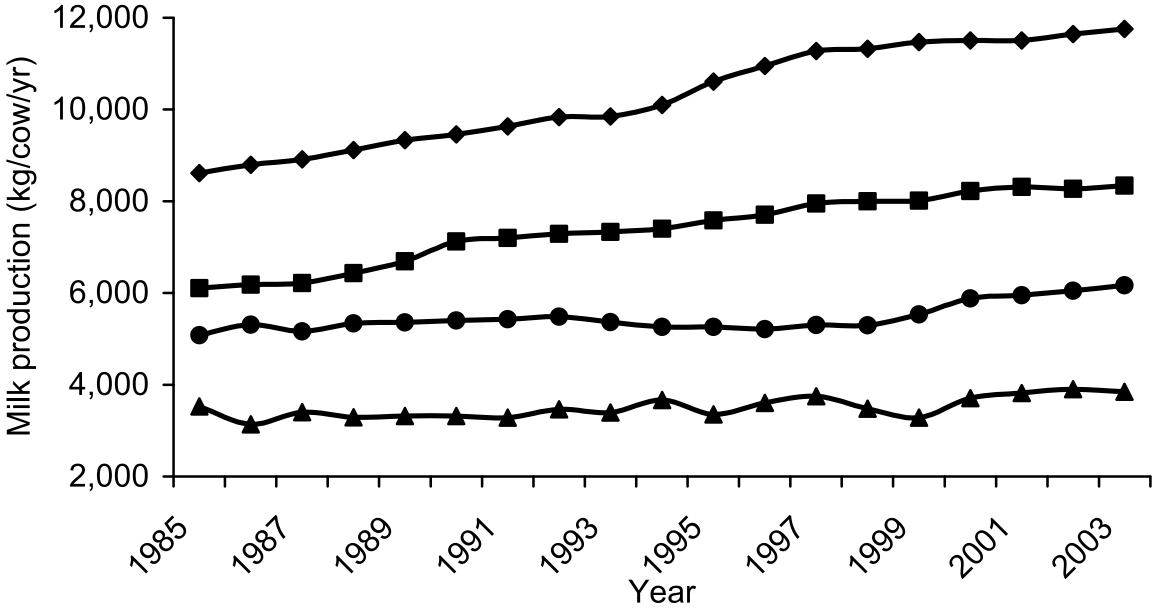

Figure 1. *Trends in milk production per cow for The Netherlands (■), United States (♦), New Zealand (▲) and Ireland (●) from 1985 to 2003 (Source: NRS, 2003; USDA, 2003; LIC, 2003; ICBF, 2003).*

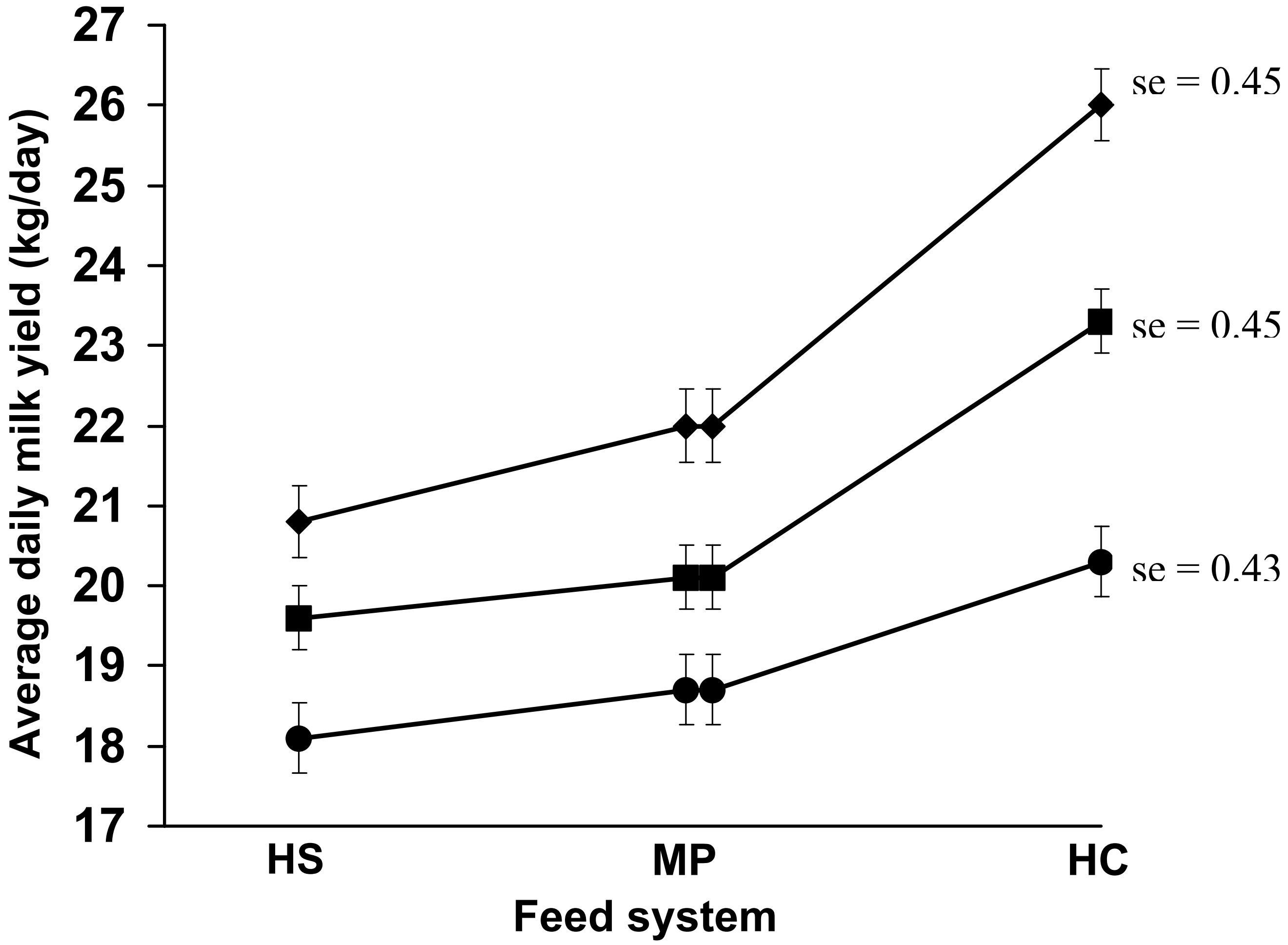

Figure 2. *Effect of interaction between strain of Holstein-Friesian cow (♦ high production; ■ high durability; ● New Zealand) and feed system (HS high stocking rate; MP Moorepark feed system; HC high concentrate) on average daily milk production during the feed system period.*