The Interaction of Strain of Holstein-Friesian Cows and Pasture-Based Feed Systems on Milk Yield, Body Weight, and Body Condition Score

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ABSTRACT

Interactions between genotype and environment are becoming increasingly important as cattle genotypes are being managed in a diverse range of environments worldwide. The objective of this study was to investigate if there is an interaction of strain of Holstein-Friesian cows (HF) by grass-based feed system that affects milk production, body weight, and body condition score. Three strains of HF were compared on 3 pasture-based feed systems over 3 consecutive years. The 3 strains of HF were: high production North American, high durability North American, and New Zealand. The 3 grass-based feeding systems (FS) were: a high grass allowance system (MPFS), a high concentrate system (HCFS), and a high stocking rate system (HSFS). There was a separate farmlet for each FS and a total of 99, 117, and 117 animals were used in yr 1, 2, and 3 respectively, divided equally between strains of HF and FS. The high production cows produced the highest yield of milk, the New Zealand the lowest, and the high durability animals were intermediate. Milk fat and protein content were higher for the New Zealand strain than for the high production and high durability strains. The New Zealand strain had the lowest body weight and the highest condition score, whereas the high durability strain had the highest body weight, and the high production strain had the lowest condition score. There was a strain $\times$ FS interaction for yield of milk, fat, and protein. The milk production response to increased concentrate supplementation (MPFS vs. HCFS) was greater with both the high production and high durability strains (1.10 kg of milk/kg of concentrate for high production; 1.00 kg of milk/kg of concentrate for high durability) than the New Zealand strain (0.55 kg of milk/kg of concentrate). The results indicate that the optimum strain of HF will vary with feed system.

(**Key words:** Holstein-Friesian strain, grass-based feed system)

Abbreviation key: FS = feed system, HCFS = high concentrate feed system, HD = high durability, HF = Holstein-Friesian, HP = high production, HSFS = high stocking rate feed system, MPFS = high grass feed system, NZ = New Zealand, PGSSH = postgrazing sward surface height.

INTRODUCTION

Milk production in Ireland is primarily based on seasonal-calving pasture-based systems. Because grazed grass is the lowest cost feed available, the objective of the system is to optimize the use of grazed grass in the diet of the lactating dairy cow (Dillon et al., 1995). This is best achieved by synchronizing calving date to the start of the grass-growing season, thereby achieving a long grazing season (February to late November) on predominantly grazed grass. The optimization of this system will greatly depend on a dairy cow that can efficiently convert this grass to a high quality milk product and is well adapted to a predominantly pasture-based seasonal-calving system.

Up to the mid1980s, the predominant breed of dairy cow in Ireland was the British Friesian. In Ireland over the last 20 yr, the use of North American Holstein-Friesian (HF) genetics has dominated, increasing from 9% in 1990 to 65% in 2001 (Evans et al., 2004). These animals have been aggressively selected for high milk production in a predominantly confinement environment (Rauw et al., 1998). The popularity of the North American HF was most likely due to its increased productivity over dairy breeds in a market that rewarded for milk volume with lesser incentive for milk solids content. However, aggressive genetic improvement within the North American HF for increased milk yield has resulted in a now well-documented negative effect on cow fertility (Pryce and Veerkamp, 2001). There is a known antagonistic genetic relationship between milk yield and reproductive traits (Evans et al., 2002; Berry et al., 2003). Pryce et al. (1998) estimated an increase of the calving interval by 5 to 10 d per 1000 kg of

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additional milk yield when selecting for milk yield only. These values are supported by the results from controlled experiments comparing genetic groups across feeding systems (Buckley et al., 2000; Kennedy et al., 2002).

In contrast, the New Zealand HF has been selected for milk production, feed efficiency, and survivability on a predominantly grass-based diet with very limited concentrate supplementation (Harris and Kolver, 2001). In New Zealand, the North American HF cows are of higher BW, produce more milk volume and protein yield, and have lower concentrations of milk fat and protein than the New Zealand HF (Harris and Kolver, 2001).

It has until recently been widely assumed that if a strain is the best for one environment (e.g., confinement), it will also be the best in all other environments. Although previous studies, across a relatively narrow range of genetic merit and/or feeding systems, have failed to show a genotype $\times$ feed system (FS) interaction, there is now evidence that high merit North American HF cows may be unable to express their full genetic potential when in a grass-based system of milk production (Kennedy et al., 2002). The importance of interactions between genotype and environment are substantial considering the diverse range of environments worldwide in which animals are now being managed.

The objective of the current study was therefore to investigate the effects of 3 strains of HF and 3 grass-based feed systems and their interactions on the milk production, BW, and BCS within Irish pasture-based systems of milk production.

MATERIALS AND METHODS

This study was carried out at Moorepark Research Centre in the Republic of Ireland over a 3-yr period (2001 to 2003).

Animals

Three strains of HF cow were compared: high production North American (**HP**), high durability North American (**HD**), and New Zealand (**NZ**). The mean pedigree index for each strain is displayed in Table 1. The pedigree index for each cow was calculated as $0.50 \times$ sire predicted difference + $0.25 \times$ maternal grandsire predicted difference + $0.125 \times$ maternal great-grandsire predicted difference. The predicted difference of the sires and maternal grandsires were from the February 2004 international evaluations of the INTERBULL Animal Center (Uppsala, Sweden) using the technique known as MACE (multiple-trait across-country evaluation).

To create the HP strain, the top 50% of HF cows in the Moorepark herd (based on pedigree index for milk production) were inseminated with semen from 5 North American HF sires. The 5 sires chosen were the 5 highest sires available in Ireland at the time based on their relative breeding index; this was the index used in Ireland based on combined predicted difference for milk, fat, and protein yields, and protein content (Irish Cattle Breeding Statistics, 1999). Therefore the HP strain was selected to illustrate what would happen if Irish dairy farmers continued to select animals aggressively for increased milk production. The average proportion of North American HF genes in the HP strain was 90%, with the remaining genes being British Friesian. To create the HD strain, the bottom 50% of HF cows in the Moorepark herds (based on pedigree index for milk production) were inseminated with semen from 5 North American HF sires, chosen on a combination of their pedigree indices for milk production, fertility, and linear (muscularity) traits. The dams used to generate this strain were representative of the HF cow that existed on most Irish dairy farms at the time. Therefore the HD strain was generated to represent a more balanced breeding policy including some indicators/fertility traits, as well as milk production traits. The average proportion of North American HF genes in the HD strain was 80%, with the remaining genes being British Friesian. The NZ animals were imported as embryos from New Zealand and implanted into 13-mo-old HF heifers at Moorepark. The NZ embryos were generated by mating high genetic merit New Zealand HF cows (expressed in the New Zealand genetic evaluation system, Breeding Worth) with 5 high genetic merit New Zealand HF sires. On average, 87.5% of the NZ strain genes were of New Zealand HF ancestry. Jersey genes contributed a maximum of 12.5%, with the remaining genes being of North American HF ancestry. The NZ strain represents a Holstein-Friesian strain that was selected within a pasture-based seasonal system, using an index that combined milk production and other traits of economic importance. The sires and dams used to generate each strain were representative of the top 10% of animals within their respective countries on overall genetic merit. The 3 strains were created not to be representative of any given existing strain of HF but merely to represent the consequences of various selection strategies on subsequent animal performance in pasture-based systems.

A total of 99, 117, and 117 animals were used in yr 1, 2, and 3, respectively, divided equally between strains of HF and FS. The number of animals of each strain of HF and FS over the 3 yr of the study is displayed in Table 2. In 2001, all 99 cows were 3 yr old; in 2002, 45 animals were 3 yr old and 72 were parity

Table 1. The mean pedigree index for 3 strains of Holstein-Friesian cows studied based on their predicted differences¹ (and SD) for milk production, survival, and calving interval.

Strain	High production	High durability	New Zealand
Milk (kg)	+194 (90.8)	+76 (61.4)	+52 (56.0)
Fat (kg)	+9.0 (2.96)	+6.3 (2.84)	+8.6 (2.66)
Protein (kg)	+8.8 (2.39)	+5.7 (1.58)	+4.2 (1.33)
Fat (g/kg)	+0.3 (0.53)	+0.7 (0.56)	+1.3 (0.58)
Protein (g/kg)	+0.4 (0.23)	+0.6 (0.30)	+0.5 (0.21)
Survival (%)	-0.5 (1.11)	+0.4 (0.51)	+1.2 (0.62)
Calving interval (d)	+0.44 (1.57)	-1.2 (0.71)	-1.6 (0.86)

¹All predicted differences were obtained from the February 2004 international evaluations of the INTERBULL Animal Centre (Uppsala, Sweden) using the MACE (multi-trait across-country evaluation). The predicted difference for each cow was calculated as $0.50 \times$ sire predicted difference + $0.25 \times$ maternal grand sire predicted difference + $0.125 \times$ maternal great grand sire predicted difference.

2; and in 2003, 9 animals were 3 yr old, 45 were parity 2, and 63 were parity 3. Fifty-nine animals remained in the same FS for the duration of the study (3 yr). All primiparous cows were on a similar feeding regimen for the first 4 wk of lactation. Animals were selected within strain into groups of 3, on the basis of calving date, milk production in the first 4 wk of lactation, and BW, and then randomly assigned to 1 of 3 systems. Once allocated, animals were retained on the same FS in subsequent lactations.

Feed Systems

There was a separate farmlet for each of the 3 systems of production. The 3 systems compared were: a high grass allowance FS typical of spring-calving herds in Ireland (**MPFS**, control); a higher concentrate system FS (**HCFS**), and a higher stocking rate system (**HSFS**). Approximately 1.0 tonne of grass silage DM per cow was required during the housing period. The MPFS had an overall stocking rate of 2.47 cows/ha, N fertilizer input of 290 kg of N/ha (from early January to late September) and received 368 kg of concentrate per cow in early lactation with the remainder of the diet coming

from grazed grass. The HCFS had a similar overall stocking rate and N input as the MPFS but a concentrate input of 1452 kg/cow. The HSFS group had similar concentrate (364 kg/cow) and N inputs as the MPFS but at a higher overall stocking rate of 2.74 cows/ha. The ingredient composition of the concentrate feed (kg/tonne as fed) was as follows: 250 kg of barley, 260 kg of corn gluten, 350 kg of beet pulp, 110 kg of soybean meal, and 30 kg of minerals plus vitamins. The MPFS and HCFS were designed to allow each strain to express its potential within each FS largely unrestricted by limitations in feed supply. The aim of the HSFS was to reduce feed allowance by increasing stocking rate and grazing HSFS pastures to a lower postgrazing surface sward height (**PGSSH**) than either the MPFS or HCFS. In all 3 yr, animals were turned out to grass during the day beginning in early February, and during day and night beginning in early March. Animals were on grass day and night until mid-November, when they were housed only at night. After December 1, they were housed day and night. During the housed period, animals were fed grass silage ad libitum. The concentrate supplementation pattern for each system is shown in Table 3. Each FS was applied immediately postpartum to all multiparous animals.

Table 2. The number of dairy cow records included in the 3-yr analysis.

Group	Strain of Holstein-Friesian ¹			Feed system ²		
	HP	HD	NZ	MP	HS	HC
No. of animals						
Yr 1	33	33	33	33	33	33
Yr 2	39	39	39	39	39	39
Yr 3	39	39	39	39	39	39
No. of lactation records						
Parity 1	51	51	51	51	51	51
Parity 2	39	39	39	39	39	39
Parity 3	21	21	21	21	21	21

¹HP = High production; HD = high durability; NZ = New Zealand.

²MP = High grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.

Grazing Management

The experimental area was a permanent grassland site containing greater than 80% perennial ryegrass (*Lolium perenne*). Fifty-four paddocks were grouped into 18 sets of 3 (balanced by location and soil type) and randomly assigned to each FS. Each system consisted of 18 paddocks of on average 0.89 ha for MPFS and HCFS, and 0.81 ha for HSFS. Within each paddock, the 3 strains grazed separate areas that were defined using temporary electric fences. In the MPFS and HCFS, the subpaddocks for the HD and NZ strains were 0.29 ha, whereas for the HP strain, paddocks were 0.31 ha. In the HSFS, both the HD- and NZ-strain subpaddocks

Table 3. Concentrate supplementation strategy¹ (kg/d per cow).

Feeding system	Calving to March 15	March 15 to March 31	April 1 to early May	Early May to end of lactation
Moorepark	6	4	2	0
High stocking rate	6	4	2	0
High concentrate	8	8	6	4

¹All primiparous animals were maintained on 7 kg/d for a pre-experimental period of 4 wk.

were 0.26 ha, and the HP-strain subpaddocks were 0.28 ha. Previous measurements had established that these allocations were likely to achieve common PGSSH for each strain. Grazing management was similar to that outlined previously (Dillon et al., 1995). Grass silage was harvested from 0.45 and 0.35 of feeding system areas in late May (first silage harvest) and early July (second silage harvest), respectively. For the remainder of the season, all of the area within the feeding system was available for grazing. A rotational grazing management system was practiced. Residency time was determined by the achievement of predetermined pasture allowances (kg/d of DM per cow) within a target PGSSH (7 to 8 cm for the MPFS and HCFS; 6 to 7 cm for the HSFS). Target PGSSH were reached in residency times that ranged from 1.5 to 2.5 d per subpaddock over the experimental period. Grazing management was accomplished by weekly monitoring of farm grass cover (O'Donovan, 2000).

The subpaddock residency time of the cows in both the HSFS and MPFS was the same, i.e., similar grazing rotation; therefore, the cows in the HSFS were forced to graze to a lower PGSSH throughout the grazing season. The grazing rotation in the HCFS moved independently to that in the MPFS and HSFS, however the HCFS group grazed to a similar PGSSH as the animals on MPFS. Pasture quality was maintained in this system by removing surplus grass throughout the experiment as silage (O'Donovan, 2000).

Animal Measurements

During the 3 yr of the study, individual milk yields were recorded on 5 consecutive days/week. The milk fat, protein, and lactose concentrations were determined using a Milkoscan 203 (Foss Electric DK-3400, Hillerød, Denmark) from successive morning and evening samples collected once weekly. The BW of each animal was recorded weekly. Each BW was recorded electronically, using portable weighing scales and Winweigh software package (Tru-Test Ltd., Auckland, New Zealand). The scales were calibrated weekly against known weights. The BCS was recorded every 3 wk during the lactation on a 0-to-5 scale (0 = emaciated, 5 = extremely fat) with

increments of 0.25 as outlined by Lowman et al. (1976). The first BW and BCS data were recorded at 24 h post-partum.

Feed Measurements

Pregrazing herbage yield (above 4 cm horizon) was determined on each grazing paddock based on 4 strips (0.80 m wide; 4.5 to 5.5 m long) of grass cut with an Agria mower (Agria-Werke GmbH, Mockmuhl/Wurt, Germany). The grass from each strip was weighed and sampled and a subsample was dried overnight at 90°C for DM determination. The remaining herbage samples from each paddock were bulked and a further subsample taken (~100 g) and freeze-dried and used for chemical analysis.

During each rotation, 30 pregrazing sward surface heights were recorded for each strain within each paddock immediately before grazing with a further 30 post-grazing sward surface heights taken immediately after grazing (Hutchings, 1991).

Chemical analysis. The composite herbage samples for each week were analyzed for modified acid detergent fiber (Clancy and Wilson, 1966), OM digestibility (Morgan et al., 1989), and Kjeldahl N. Similarly, in periods of silage supplementation, a composite grass silage sample for each week was analyzed for residual moisture, DM digestibility (Tilley and Terry, 1963), Kjeldahl N, modified ADF, and NDF (Van Soest et al., 1966). Concentrates were sampled weekly, bulked over each month, and analyzed for DM, total N, crude fiber, NDF, oil, and ash.

Data Handling

The data set was divided into 2 periods for the purpose of statistical analysis. Firstly, the production, BW, and BCS data were analyzed over the complete lactation (wk 3 of year to wk 53, inclusive) in all 3 yr. A second data set was created to examine the performance of each group exclusively during the period in lactation when the 3 feeding systems were in place (wk 10 of year to wk 45, inclusive) in all 3 yr. In early lactation (February and March) and late lactation (mid-Novem-

ber/December), when cows were housed by night or by night and day, the various feed systems were not in place.

Statistical Analysis

Data were analyzed using a repeated measures model (PROC MIXED) described below using the statistical procedures of SAS (SAS Institute, 2002). Cow was included as a random effect, and year, parity, strain of HF, and feed system were included as fixed effects. Each year, the newly introduced animals were selected within strain and parity on calving date and pre-experimental milk yield. Animals present from the previous year were maintained in the same feed system. To improve the accuracy of the model, pre-experimental milk yield, BW, and BCS were used as covariates specific to the traits being analyzed. The following model was used:

$$Y_{ijkl} = \mu + \text{cov } e + R_i + L_j + S_k + F_l \\ + LS_{jk} + SF_{kl} + LF_{jl} + LSF_{jkl} + e_{ijkl},$$

where Y_{ijkl} = the performance of the animal in yr i of parity j and strain k on feed l , R_i = the effect of i th yr ($i = 1, 2, 3$), L_j = parity ($j = 1, 2, 3$), S_k = strain of HF ($k = \text{HP, HD, or NZ}$); F_l = the effect of the l th feed system ($l = \text{MPFS, HSFS, HCFS}$), and e_{ijkl} = the residual error term.

For the milk production variables, the covariates used were pre-experimental milk production, individual animal predicted difference for milk production, and calving date for each animal on the study. Models for BW and BCS included covariates for pre-experimental BW and condition score, gestation length, and calving date. Owing to the differences between strains in terms of the pre-experimental values, these covariates were centered within strain before inclusion. That is, the deviations from the strain mean were used as the covariates. The incorporation of individual animal covariates within the model reduced the residual error term, therefore explaining more of the variation within strains.

Orthogonal contrasts (Snedecor and Cochran, 1980) were used to make a number of comparisons. The PRODL contrast refers to the comparison of animals selected purely for high milk production potential (HP strain) with animals that are not selected aggressively for milk production (HD and NZ strains) [PRODL; HP vs. (HD + NZ)/2]. The LOWP contrast refers to the comparison of exclusively lower production groups, therefore comparing the lower production North American HF (HD strain) to the NZ strain (LOWP; HD vs. NZ). The effect of FS was determined by making the following comparisons with the MPFS (control): MPFS vs.

HSFS and MPFS vs. HCFS. The effect of strain of HF on response to stocking rate and concentrate supplementation was also tested using the Student's t -test to compare the differential in performance of each strain in the MPFS with the performance in the HSFS and HCFS during the feed system period.

RESULTS

Table 4 shows the results of the chemical analyses of the herbage, grass silage, and concentrate offered in each of the 3 yr. Data in Table 5 shows the concentrate input, pre- and postgrazing sward heights, pregrazing yield, and daily herbage allowance for each of the treatment groups for both the complete 3-yr data set and for the specific periods when the feeding systems were in place. These results show that although the 3 feed systems had similar pregrazing heights, concentrate supplementation, postgrazing sward height and daily herbage allowance did differ significantly between feed systems.

Milk Production

Complete lactation analysis. There was a significant interaction between strain of HF and FS for all milk yield variables (Table 6). There are also individual effects of strain of HF and FS evident in the data. The HP strain had the highest ($P < 0.001$) total lactation milk yield (6958 kg), the NZ strain the lowest (6141 kg) milk yield, and the HD strain was intermediate (6584 kg). The HP strain had the highest ($P < 0.001$) SCM yield (Tyrell and Reid, 1965) (6629 kg), whereas no difference was observed between the HD (6359 kg) and NZ strains (6278 kg). The HP strain had the highest peak milk yield (34.8 kg), total protein (241 kg), and total lactose yields (326 kg), with the NZ strain the lowest (30.2, 224, 288 kg, respectively), and the HD strain was intermediate (32.8, 235, 308 kg, respectively). The HP strain also produced more ($P < 0.001$) fat over the lactation (279 kg) with no significant difference between the HD (268 kg) and NZ strains (275 kg).

Similarly, FS had a significant effect on all milk production parameters. The cows in HCFS produced the highest ($P < 0.001$) yield of milk (7199 kg), SCM (7040 kg), peak milk (34.4 kg), protein (259 kg), and lactose (341 kg), with HSFS the lowest (6133, 6025, 31.2, 216, and 285 kg, respectively), with the MPFS being intermediate (6352, 6200, 32.1, 225 and 296 kg, respectively). The cows in the HCFS also produced the highest ($P < 0.001$) yield of fat over lactation (296 kg) with no significant difference between the MPFS and HSFS (265 and 260 kg, respectively). Significant interactions

Table 4. Chemical composition of grass, grass silage, and concentrate (Conc) offered in yr 1, 2, and 3.

	Yr 1			Yr 2			Yr 3		
	Grass	Conc	Grass silage	Grass	Conc	Grass silage	Grass	Conc	Grass silage
DM (g/kg)	...	921 (4.3)	898 (2.9)	...	92.5 (5.3)	887 (7.4)	...	928 (5.1)	901 (9.2)
DM composition (g/kg)									
DM digestibility	...	...	722 (29.8)	...	...	703 (28.5)	...	...	708 (20.5)
OM digestibility	798 (1.9)	...	...	795 (12.2)	...	...	806 (8.0)	...	...
CP	168 (6.0)	182 (17.7)	137 (10.5)	166 (2.0)	179 (12.6)	119 (10.3)	178 (5.51)	190 (8.9)	130 (15.6)
Crude fiber	...	78.9 (10.2)	...	...	91.3 (9.13)	...	...	84.9 (13.4)	...
MADF ¹	277 (15.6)	...	335 (14.6)	268 (1.2)	...	357 (15.9)	269 (10.9)	...	346 (12.1)
NDF	446 (3.6)	349 (17.3)	491 (19.8)	445 (3.9)	281 (14.2)	558 (19.9)	463 (7.11)	316 (25.7)	514 (62.9)
Ash	83.0 (0.77)	88.0 (7.67)	80.3 (6.75)	85.7 (3.0)	89.6 (9.23)	66.0 (6.16)	83.7 (1.49)	88.7 (6.51)	67.0 (1.41)

¹MADF = Modified ADF.

between strain of HF and FS were observed for all milk yield variables.

Parity had a significant effect on total lactational milk production (significance levels are included in Table 6). Third-parity cows had the highest ($P < 0.001$) yield of milk (7436 kg), SCM (7449 kg), peak daily milk (37.1 kg), fat (307 kg), protein (259 kg), and lactose (340 kg), the first-parity cows had the lowest ($P < 0.001$) (5533, 5322, 26.8, 233, 199, and 266 kg, respectively), and the second-parity cows were intermediate for all variables (6850, 6698, 33.7, 281, 242, and 317 kg, respectively). First-parity animals also had lower ($P < 0.01$) protein concentration (35.2 g/kg) compared with animals of second and third parity (35.9 and 36.0 g/kg, respectively).

Feed system period analysis. During the feed system period, the interaction of strain of HF and FS as well as effects of strain of HF and FS were observed (Table 7). Feed system had a significant effect on all variables measured. The cows in the HCFS produced the highest ($P < 0.001$) daily yield of milk (23.4 kg/d), SCM (22.6 kg/d), fat (933 g/d), protein (851 g/d), and lactose (1111 g/d), the cows in the HSFS the lowest ($P < 0.05$) (19.5 kg, 18.9 kg, 806 g, 694 g, and 908 g, per d, respectively), and that of the cows in MPFS was intermediate (20.2 kg, 19.7 kg, 831 g, 726 g, and 939g, per day, respectively). The HCFS group had lower ($P < 0.01$) fat composition (40.5 g/kg) compared with the HSFS group (41.6 g/kg), with MPFS intermediate (41.1 g/kg). The cows in the HCFS produced the highest protein and lactose content (36.8 and 47.5 g/kg, respectively), with no significant difference between the MPFS (36.1 and 46.4 g/kg, respectively) and HSFS (36.0 and 46.7 g/kg, respectively).

Significant strain $\times$ FS interactions were observed for daily yield of milk, SCM, fat, protein, lactose, and protein composition. The interaction of strain of HF and FS for daily milk production is shown in Figure 1. The reduction in daily milk production in the HSFS was similar for both the HD and NZ strains (reducing daily milk yield by 0.5 and 0.6 kg/d, respectively, relative to the MPFS). In comparison, greater ($P < 0.05$) sensitivity to the HSFS was observed among the HP strain over this period, with average daily milk production being reduced by 1.2 kg/d. A greater ($P < 0.05$) reduction in daily SCM, fat, and lactose yield was observed among the HP strain (with reductions in daily production of 1.3 kg, 70 g, and 58 g, respectively) compared with the HD (0.3 kg, 24 g, and 32 g) and NZ strains (0.7 kg, 16g, and 37 g, respectively). The HSFS had a similar affect on all strains in terms of protein yield and milk composition.

The milk production of the NZ strain is less sensitive to concentrate input compared with the HP and HD

Table 5. Differences between feed systems¹ (MP, HS, HC) in concentrate input and pasture management in 3 strains of Holstein-Friesian² (HP, HD, NZ).

	HP			HD			NZ			SEM	P ³	
	MP	HS	HC	MP	HS	HC	MP	HS	HC		S	F
Complete lactation												
Total concentrate input (kg of DM/ cow)	314	299	1257	316	317	1270	321	330	1262	127.2		***
Feed system period												
Daily concentrate input (kg/d DM/cow)	0.0	0.0	3.7	0.0	0.0	3.7	0.0	0.0	3.7	0.09		***
Pregrazing sward height (cm)	21.9	22.0	21.8	21.8	22.0	21.9	21.9	21.9	21.9	3.62		
Postgrazing sward height (cm)	7.8	7.4	7.6	7.8	7.4	7.6	7.8	7.3	7.6	1.26		***
Daily herbage allowance (kg/d of DM/cow)	30.0	25.5	26.4	28.1	23.9	24.7	28.1	23.9	24.7	0.49	***	***

¹Feed systems: MP = high grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.

²Strains: HP = high production; HD = high durability; NZ = New Zealand.

³Effects: S = effect of strain of Holstein-Friesian; F = effect of feed system. There was no significant strain of HF × feed system interaction detected.

*** $P < 0.001$.

groups. Table 8 shows the effect of strain of HF on milk production response to increased concentrate (MPFS vs. HCFS) during the feed system period. The milk production response to increased concentrate supplementation was significantly greater for the HP and HD strains (1.08 and 1.00 kg of milk/kg of concentrate, respectively) than the NZ strain (0.43 kg of milk/kg of concentrate). Similar trends were observed in terms of daily SCM, protein, and lactose yields. The HD strain displayed a greater response in fat yield compared with the HP and NZ strains.

BW and BCS

Complete lactation analysis. The effects of strain of HF and FS on BW and BCS over the entire lactation are displayed in Table 9. Immediately postpartum, both the HP and HD strains (553 and 556 kg, respectively) were heavier ($P < 0.001$) than the NZ strain (517 kg). The HD strain was heaviest ($P < 0.05$) at nadir BW, and at drying-off (500 and 596 kg, respectively), the NZ strain the lightest (463 and 553 kg, respectively), and the HP strain was intermediate (491 and 570 kg, respectively). The NZ strain had the highest ($P < 0.001$) BCS immediately postpartum (3.37), at nadir BCS (2.84), and at drying-off (3.13), the HP strain the lowest ($P < 0.01$) (3.17, 2.45, and 2.68, respectively), and the HD strain was intermediate (3.24, 2.65, and 2.93, respectively). Strain of HF had no significant effect on BW change from calving to nadir BW, however the HP strain lost significantly more body condition (−0.73) from calving to nadir, compared with the HD (−0.59) and NZ strains (−0.55). The HD strain had a greater ($P < 0.001$) BW gain from nadir BW to the end of lactation (95.7 kg), compared with the HP (82.8 kg) and NZ strains (86.1 kg), with no difference in condition score gain between strains.

Feed system had a significant effect on BW and BCS. The cows in the HCFS were heaviest ($P < 0.05$) at nadir BW (491 kg) and at drying-off (586 kg), whereas no difference was observed between the MPFS and HSFS at nadir BW (482 and 481, respectively) or at drying-off (567 and 566, respectively). The HCFS had the highest ($P < 0.001$) nadir BCS (2.77) and BCS at drying-off (3.03), with the MPFS and HSFS groups having the same BCS at nadir (2.59) and at drying-off (2.84 and 2.87, respectively). Cows in the HCFS gained more BW between nadir BW and drying-off (96.0 kg) compared with the HSFS and MPFS (84.0 and 83.3 kg, respectively). Similarly, the cows in the HCFS lost significantly less ($P < 0.05$) BCS from calving to nadir (0.51), compared with HSFS and MPFS (0.64 and 0.72, respectively).

Animals of third parity were heaviest ($P < 0.001$) immediately postpartum, at nadir BW, and at drying-off (580, 522, and 605 kg, respectively), first-lactation animals the lightest (501, 438, and 531 kg, respectively), and second-lactation animals were intermediate (545, 495, and 573 kg, respectively). Primiparous animals had the highest BCS immediately postpartum (3.26), and at drying-off (2.93), whereas the second-parity animals had the lowest BCS immediately postpartum (3.18), and the third-parity animals had the lowest BCS at drying-off (2.87). Second-parity animals had lower ($P < 0.05$) BW and BCS loss between calving and nadir (50.6 kg and 0.56, respectively) compared with the primiparous (63.5 kg and 0.63, respectively) and third-parity animals (57.8 kg and 0.69, respectively).

Feed system period analysis. Strain of HF, FS, and parity had significant effects on BW and BCS during the feed system period (Table 10). The cows in the HCFS were heaviest at the beginning and end of the feed system period (524 and 583 kg, respectively), and had

Table 6. Effect of strain of Holstein-Friesian¹ (HP, HD, NZ), feed system² (MP, HS, HC), and interaction between strain of HF and FS on milk production over the complete lactation.

	HP			HD			NZ			SEM	Significance ³					
	MP	HS	HC	MP	HS	HC	MP	HS	HC		S	F	L	S × F	PRODL	LOWP
Total milk yield (kg/cow)	6799	6283	7877	6408	6176	7360	6039	5940	6444	124.8	***	***	***	***	***	***
SCM ⁴ yield (kg/cow)	6489	5999	7376	5976	6012	7074	6120	6065	6648	104.5	***	***	***	***	***	***
Maximum yield (kg/d per cow)	34.5	32.7	37.2	32.1	31.1	35.2	29.8	29.8	31.0	0.53	***	***	***	*	***	***
Fat yield (kg/cow)	277	256	304	252	257	295	267	269	288	5.1	*	***	***	**	***	***
Protein yield (kg/cow)	234	217	272	221	219	264	219	213	240	3.6	***	***	***	***	***	***
Lactose yield (kg/cow)	315	291	371	289	288	346	282	277	305	6.0	***	***	***	***	***	***
Milk composition (%)																
Fat	40.6	41.0	40.0	40.9	41.1	40.1	43.9	45.6	44.5	0.07	***	*	†		***	***
Protein	34.5	34.8	35.4	35.6	35.5	35.8	36.5	36.1	37.2	0.04	***	*	**		***	**
Lactose	46.3	46.6	47.7	46.6	46.7	47.1	46.7	46.6	47.5	0.02		***				

¹Strains: HP = high production; HD = high durability; NZ = New Zealand.²Feed systems: MP = high grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.³Effects: S = effect of strain of Holstein-Friesian; F = effect of feed system; L = effect of parity; S × F = effect of interaction between strain of Holstein-Friesian and feed system; PRODL = linear contrast of the HP group with low production groups [HP vs. (HD + NZ)/2]; LOWP = linear contrast of HD and NZ strains (HD vs. NZ).⁴SCM = Solids-corrected milk.****P* < 0.001, ***P* < 0.01, **P* < 0.05, †*P* < 0.10.**Table 7.** Effect of strain of Holstein-Friesian¹ (HP, HD, NZ), feed system² (MP, HS, HC), and parity on milk production during the feed system period.

	HP			HD			NZ			SEM	Significance ³					
	MP	HS	HC	MP	HS	HC	MP	HS	HC		S	F	L	S × F	PRODL	LOWP
Yield																
Milk (kg/d per cow)	22.0	20.8	26.0	20.1	19.6	23.3	18.7	18.1	20.3	0.45	***	***	***	**	***	***
SCM ⁴ (kg/d per cow)	20.9	19.6	24.3	19.2	18.9	22.1	19.0	18.3	20.9	0.32	***	***	***	**	***	*
Fat (g/d per cow)	887	817	980	821	797	928	818	802	891	16.7	***	***	***	*	***	***
Protein (g/d per cow)	774	722	911	742	700	864	697	659	778	12.9	***	***	***	**	***	***
Lactose (g/d per cow)	1032	974	1245	943	911	1119	874	837	970	22.1	***	***	***	**	***	***
Milk composition (%)																
Fat	39.4	39.6	38.6	40.3	40.5	39.3	43.6	44.9	43.5	0.08	***	†			***	***
Protein	34.6	35.2	35.6	36.3	36.0	36.4	37.4	36.8	38.4	0.04	***	*		*	***	***
Lactose	46.3	46.9	47.6	46.4	46.7	47.2	46.5	46.4	47.7	0.03		***				

¹Strains: HP = high production; HD = high durability; NZ = New Zealand.²Feed systems: MP = high grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.³Effects: S = effect of strain of Holstein-Friesian; F = effect of feed system; L = effect of parity; S × F = effect of interaction between strain of Holstein-Friesian and feed system; PRODL = linear contrast of the HP group with low production groups [HP vs. (HD + NZ)/2]; LOWP = linear contrast of HD and NZ strains (HD vs. NZ).⁴SCM = Solids-corrected milk.****P* < 0.001, ***P* < 0.01, **P* < 0.05, †*P* < 0.10.

Table 8. Effect of strain of Holstein-Friesian¹ on milk production response to concentrate supplementation during the feed system period.

	HP	HD	NZ	P
Daily milk yield response (kg/kg)	1.08 ^a	1.00 ^a	0.43 ^b	*
Daily SCM ² yield response (kg/kg)	0.92 ^a	0.86 ^a	0.51 ^b	*
Daily fat yield response (g/kg)	25 ^a	38 ^b	20 ^a	*
Daily protein yield response (g/kg)	37 ^a	42 ^a	22 ^b	*
Daily lactose yield response (g/kg)	58 ^a	56 ^a	26 ^b	**

^{a,b}Means with different superscripts within the same row are significantly different.

¹HP = High production; HD = high durability; NZ = New Zealand.

²SCM = Solids-corrected milk.

** $P < 0.01$, * $P < 0.05$.

the highest BW gain over the 27-wk FS period (60 kg). The HSFS were lighter ($P < 0.10$) than the MPFS at wk 1 (508 and 514 kg, respectively), and at wk 26 (563 and 566 kg, respectively). The BW change did not differ between the HSFS and MPFS over the period (54.5 and 52.0 kg, respectively). The cows in the HCFS had higher BCS at the start and end of the FS period (2.90 and 3.03, respectively), compared with HSFS (2.82 and 2.87, respectively) and MPFS (2.82 and 2.83, respectively). The HCFS had the highest ($P < 0.001$) BCS gain over the period (0.15), with no difference between the MPFS (−0.02) and HSFS (0.04) systems.

The interaction of strain of HF and FS approached significance ($P = 0.14$) for BW change from wk 1 to 26 postpartum due to the higher BW gain exhibited by the HD and NZ strains relative to the HP group in both the MPFS and HCFS.

DISCUSSION

A farmlet study allows greater feeding and management control than a large population study, where it is difficult to account for the influences of on-farm decisions. The limitations of the former analysis arise from the lack of replication relative to population studies. Such limitations are overcome by repeating the experiment over a number of years. This data set provides a unique opportunity to investigate the performance of divergent strains of HF dairy cow in 3 pasture-based systems of milk production. By analyzing the data set exclusively during the feed system period, the biological significance of any interaction between strain of HF and FS can be quantified accurately.

A genotype × environment interaction occurs when animals differ in their ability to perform in different environments (Falconer, 1990). A number of studies have shown a genotype × environment interaction in dairy production systems (Veerkamp et al., 1994; Boettcher et al., 2003). The existence of a genotype ×

Table 9. Effect of strain of Holstein-Friesian¹ (HP, HD, NZ), feed system² (MP, HS, HC), and parity on BW and BCS over the complete lactation.

	HP			HD			NZ			Significance ³				
	MP	HS	HC	MP	HS	HC	MP	HS	HC	SEM	S	F	L	PRODL
BW postcalving (kg)	557	553	548	556	546	568	511	518	521	6.0	***	***	***	***
BW at drying-off (kg)	557	569	584	593	582	613	550	546	562	6.9	***	***	***	***
BW at nadir (kg)	490	486	496	497	492	512	460	464	464	5.2	***	*	***	*
BCS postcalving	3.20	3.14	3.16	3.32	3.16	3.26	3.39	3.37	3.38	0.040	***	*	***	***
BCS at drying-off	2.58	2.65	2.82	2.87	2.88	3.05	3.07	3.09	3.24	0.057	***	*	***	***
BCS at nadir	2.35	2.43	2.56	2.61	2.56	2.79	2.82	2.77	2.94	0.049	***	***	*	***
BW change														
Calving to nadir (kg)	65.7	67.5	50.5	55.6	57.0	55.0	52.4	55.2	56.7	5.28	***	**	*	**
Nadir to drying-off (kg)	67.7	80.1	90.0	93.3	89.9	102.7	91.0	79.9	95.3	5.16	***	**	*	**
BCS change														
Calving to nadir	−0.85	−0.73	−0.60	−0.69	−0.63	−0.46	−0.61	−0.57	−0.47	0.045	***	***	*	***
Nadir to drying-off	0.21	0.19	0.27	0.22	0.28	0.19	0.24	0.28	0.28	0.042	***	***	*	***

¹Strains: HP = high production; HD = high durability; NZ = New Zealand.

²Feed systems: MP = high grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.

³Effects: S = effect of strain of Holstein-Friesian; F = effect of feed system; L = effect of parity; PRODL = linear contrast of the HP group with low production groups [HP vs. (HD + NZ)/2]; LOWP = linear contrast of HD and NZ strains (HD vs. NZ).

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Table 10. Effect of strain of Holstein-Friesian¹ (HP, HD, NZ), feed system² (MP, HS, HC), and parity on BW and BCS during the feed system period.

	HP			HD			NZ			Significance				
	MP	HS	HC	MP	HS	HC	MP	HS	HC	SEM	S	F	L	G × F
BW at start of wk 1 (kg)	517	510	530	533	524	546	491	490	496	5.3	**	***	***	***
BW at finish of wk 26 (kg)	556	567	582	591	579	609	549	543	560	6.8	***	***	***	***
BCS at start of wk 1	2.65	2.67	2.72	2.81	2.76	2.89	2.99	3.02	3.08	0.051	***	†	***	***
BCS at finish of wk 26	2.56	2.65	2.82	2.86	2.88	3.05	3.07	3.09	3.23	0.057	***	***	***	***
BW change (wk 1 – 26) (kg)	40	54	53	57	56	63	59	53	62	4.0	**	*	**	0.14
BCS change (wk 1 – 26)	–0.12	–0.04	0.13	0.00	0.10	0.15	0.06	0.07	0.15	0.039	**	***	***	*

¹Strains: HP = high production; HD = high durability; NZ = New Zealand.²Feed systems: MP = high grass feed system; HS = high stocking rate feed system; HC = high concentrate feed system.³Effects: S = effect of strain of Holstein-Friesian; F = effect of feed system; L = effect of parity; G × F = effect of interaction between genotype and concentrate feed level; PRODL = linear contrast of the HP group with low production groups [HP vs. (HD + NZ)/2]; LOWP = linear contrast of HD and NZ strains (HD vs. NZ).*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

environment interaction can be in the form of a “scaling effect,” where the difference in the level of performance between 2 genotypes is smaller at a low level than a high feeding level, or a “re-ranking” where 2 genotypes rank differently in contrasting feeding systems. It is only possible to investigate the “scaling effect” with the present data set.

Kennedy et al. (2003) showed that with a high proportion of forage in the diet, high genetic merit dairy cows are not capable of eating much more than low genetic merit dairy cows, whereas on high concentrate diets, high genetic merit cows have the advantage of higher DM intakes. Hence, the differences in milk yield between genotypes are smaller in a high grass diet because intake is limited by constraining factors in the diet such as physical bulk, or by the relatively slow rate of intake that can be achieved by grazing cows compared with a system that entails a high level of concentrate supplementation.

Effect of Strain

The overall level of milk production achieved in the present study is similar to that obtained in previous studies at this center (Kennedy et al., 2002). Kennedy et al. (2002) showed total lactation milk yields of 6421 and 7389 kg with medium and high genetic merit HF cows, respectively, on low concentrate, and 7196 and 8461 kg, respectively, on a high concentrate system. These levels of production are much higher than that achieved in other pasture-based systems with high genetic merit cows. Kolver (2001) obtained 4678 kg of milk per cow with high genetic merit North American HF cows in a New Zealand grazing system with a low stocking rate. The milk protein composition achieved in the present experiment may be considered high for cows on a high forage system. Similar milk composition has been reported previously at this center (Buckley et al., 2000; Kennedy et al., 2002) when animals have been given access to high quality perennial ryegrass swards over a long grazing season.

The difference in observed milk production between the HP strain and the 2 low production strains (HD and NZ) is in agreement with the differences in predicted difference for milk, and similar to that observed in previous studies (Buckley et al., 2000; Boettcher et al., 2003). This higher milk production has been achieved successfully because milk production is a highly heritable selection criterion (Evans et al., 2002). The lower overall milk production and higher composition of the NZ strain compared with North American strain has also been observed previously (Kolver et al., 2000). Kolver (2001) showed that in New Zealand, North American-derived Holstein-Friesian cows were heav-

Figure 1. Effect of interaction between strain of Holstein-Friesian cow and feed system (HS = high stocking rate; MP = high grass; HC = high concentrate) on average daily milk production during the feed system period for the high production (◆), high durability (■), and New Zealand (●) Holstein-Friesian strains.

ier, produced more milk volume and protein yield, and had lower concentration of fat and protein than New Zealand-derived Holstein-Friesian cows.

Until recently, the breeding schemes of the North American HF cow population within Europe have been based solely on increased milk production. Such breeding programs increase the gap between energy intake and output in early lactation. For this reason a greater mobilization of BW and BCS is expected among the HP strain. The higher BW of the HD strain relative to the HP animals is understandable given their lower level of milk production, coupled with their higher muscularity.

The reduced BCS displayed by the HP cows is also expected because many studies have shown lower BCS in animals selected for higher milk yield (Berry et al., 2003) and because the correlated response in feed intake in early lactation, due to selection for milk yield, can cover only 40 to 48% of the extra requirement (Veerkamp et al., 1994). Selection on milk yield alone is expected to increase the mobilization of body reserves in early lactation, the magnitude and duration of which is related to reduced health and fertility (Buckley et al., 2003). Many studies have shown that cows genetically superior for milk production tend to have genetically lower BCS throughout lactation and greater BCS

change in early lactation than those of lower genetic merit (Buckley et al., 2000). Dechow et al. (2002) suggests that as cows are selected for higher milk production and become genetically thinner, the amount of body condition lost postpartum is likely to increase at any given level of BCS at parturition.

The lower BW and higher BCS of the NZ strain is a consequence of the negative weighting on milk volume and BW within the New Zealand Breeding Worth index (Harris, 1998). Previous studies in New Zealand showed that offspring of North American HF sires were heavier and taller than the New Zealand HF. Kolver et al. (2000) showed that North American HF heifers had a higher BW and they were unable to maintain acceptable body condition and BW on a pasture-based diet when compared with the New Zealand Holstein HF.

Effect of FS

The higher total lactation milk, SCM, fat, protein, and lactose yield achieved with the HCFS group is expected, given the large increase in energy supply with this FS. This is consistent with previous studies, which showed that total DMI increased with increasing pro-

portion of concentrate in the diet (Bargo et al., 2002). The decline in milk fat content observed with HCFS was in agreement with previous findings (Bargo et al., 2002), and can be largely attributed to the reduced fiber content in the diet. The general increase in milk protein content on HCFS is likely attributable to increased energy intake and has been reported previously (Dillon and Crosse, 1997; Bargo et al., 2002).

The significant genotype $\times$ environment interaction observed for milk production over the complete lactation and during the feed system period agrees with similar farmlet studies (Kennedy et al., 2002), as well as large database studies (Boettcher et al., 2003). These interactions are explained by the large difference in response to additional energy intake between strains. The higher milk production response by the HP animals to a greater grass allowance in the MPFS demonstrates their greater nutritional stress, relative to the lower production strains. Differences in the response to additional energy input have been attributed to such factors as physiological stage, body condition, and milk production potential. As an animal approaches its maximum milk production potential, an increasing proportion of the energy supplied is retained as body lipid (Broster et al., 1985).

In the present study, the low response to concentrate supplementation from the NZ strain coupled with their higher BCS suggests that these animals achieved a greater proportion of their potential milk production in the MPFS than the HP strain. Coulon and Remond (1991) found that when energy requirements are not being met, concentrate supplementation appreciably influences the energy balance of the animal resulting in increased animal performance. Although body reserves usually buffer shortfalls in energy supply, prolonged mobilization is not possible due to innate metabolic adaptations within the animal (homeostasis). Consequently, high yielding cows are of lower body condition and display a more pronounced response to concentrate supplementation, as their energy demands for milk production are not fully met on a predominantly pasture-based diet. Many other studies using high genetic merit dairy cows for milk production have shown large responses to concentrate on pasture-based systems (Delaby et al., 2001; Kennedy et al., 2002).

The interaction of strain of HF and FS approached significance for BW change. This is mainly due to the lower BW gain of the HP animals in both the MPFS and HCFS. The lower BW gain among the HP strain over the feed system period may have arisen as a consequence of the higher milk production relative to the HD group during the feed system period. The energy intake resulting from increased grass allowance (in the MPFS) and additional concentrate supplementation (in the

HCFS) resulted in a larger milk production response in these systems rather than in BW gain. The lack of agreement between BW and BCS change has been observed previously (Sutter and Beever, 2000). These authors concluded that BW change was an inadequate index of body tissue mobilization in early lactation as it might be biased by increased gut content or water repletion of body tissue.

Historically, genetic selection in dairy cattle has been within country. However, global selection can increase the rate of genetic progress in dairy cattle by up to 17% compared with within-country selection (Lohuis and Dekkers, 1998). However, such success has in turn raised new doubts relating to the problem of genotype $\times$ environment interaction, as exemplified in this study. In a seasonal pasture-based system, characteristics other than milk production, such as reproductive performance and animal health, are important (Veerkamp et al., 2002). Ultimately, the optimum cow for pasture-based systems can only be identified by combining all traits (production and health) of economic significance in a weighted index of economic merit and choosing sires at the top of this index. The results of this study show that accurate prediction of milk production performance must be based on knowledge of both dairy cow genotype and feed environment.

CONCLUSIONS

Strain of HF, FS, parity, and the interaction of strain and FS had a significant effect on the milk production of spring-calving cows in pasture-based systems. The data shows that in a grass-based system, aggressive selection for increased milk production (HP strain) in the North American HF has resulted in an animal with higher milk production, and greater response to additional concentrate supplementation but with greater loss of BW and BCS postcalving. 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 BW, and highest BCS. The HD strain was intermediate for milk production and composition, had the highest BW, and was intermediate for BCS. The existence of strong interactions between strain of HF and FS for milk production demonstrates that the optimum strain of HF will vary with system of milk production. These results show that the prediction of animal performance must be based on knowledge of both feed system and genotype.

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