Genotype by Environment Interaction for Yield and Somatic Cell Score with Alternative Environmental Definitions

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ABSTRACT

Differential genetic expression in high and low opportunity Sicilian Holstein-Friesian and Brown Swiss herd environments was investigated using endogenous and exogenous variables in a set of three definitions. Results of genetic by environmental interaction were compared using alternative environmental definitions: within herd-year standard deviation for mature equivalent milk yield (HYSD), detectable incidence of normal vs. abnormal (peakless) lactation and herds clustered by causal relationships from high and low frequency use of nutrition, milking, health and animal handling practices. Data for genetic analysis consisted of first-lactation standardized yields of milk, fat and protein, and weighted somatic cell score for 8897 daughters of 825 Holstein-Friesian sires and 1143 daughters of 220 Brown Swiss sires. Components of covariance, heritabilities, and genetic correlations were estimated using bivariate and multivariate sire models for average and contrasting environments for each definition. Sire variances for yields were consistently smaller in the low opportunity environments of both breeds. Except for differential incidence of abnormal lactation in Friesian herds, correlated yield response in less privileged environments was 0.41 to 0.81 as much as in high opportunity environments, a substantial loss. Genetic correlations between HYSD environments for yield traits of Friesian were 0.48 to 0.66 but exceeded 0.80 for other definitions. Less correlated response in somatic cell score was also predicted for environments with low use of yield-enhancing practices (0.66 for Friesian and 0.61 for Brown Swiss), which may have resulted from less health care and poorer milking management. Therefore, unfavorable management interactions likely foster unequal gains from selection in contrasting environments defined exogenously or by incidence of peakless lactation. Conversely, greater genetic as well as phenotypic response is expected from additional inputs of nutrition, health care and milking management.
(**Key words:** genotype × environment interaction, heterogeneous genetic variance, milk yield, environmental definitions)

Abbreviation key: G×E = genotype by environment interaction, **HYSD** = herd-year standard deviations, **ME** = Mature equivalent, **WSCS** = weighted somatic cell score.

INTRODUCTION

Potential genotype by environment interaction (**G×E**) in milk production has been mostly studied with environments arbitrarily defined by country, region, and herd phenotypic performance. Two criteria especially have been used to discriminate productive opportunity: herd mean milk yield per cow and its phenotypic variance. Kolmodin and co-workers (2002) recently used herd-year mean performance to define a continuous environmental gradient, or reaction norm, to circumvent limitations of genetic connectedness between countries, which potentially enhances the likelihood of detecting G×E. However, differentiation by mean yield is analogous to selection on herd means, which may result in biased estimates of genetic and residual variances (Famula, 1989). Within herd-year-season or herd-year standard deviations (**HYSD**) for milk yield have usefully discriminated herd environments in various geographic regions because heterogeneous phenotypic variances consistently predisposed unequal genetic responses, presumably because productive opportunity varies accordingly (Carvalheira et al., 1998; Cienfuegos-Rivas et al., 1999; Costa et al., 2000; Short et al., 1990; Stanton et al., 1991b; Meinert et al., 1988; Meinert et al., 1992). A drawback of HYSD definition of production environments is that it relies on an endogenous variable potentially correlated with yield response (i.e., the outcome). Production conditions also have been characterized by clustering herds primarily by endogenous descriptors (e.g., HYSD, peak yield, days to peak yield, herd size) to predict sire breeding values

for alternative systems but only heritabilities and genetic correlations were reported (Weigel and Rekaya, 2000; Zwald et al., 2001). We are unaware of reports of genetic components of covariance and expected correlated responses for contrasting environments defined by causal relationships (e.g., inputs and practices) with animal response.

Licitra and collaborators (1998) found substantial peakless lactations in herds in Mediterranean southeastern Sicily (Italy) lacking normal detectable ascent to peak milk yield followed by a rapid (convex) decline. These abnormal outcomes signified substantial sacrifices in milk production with restricted within-herd variation. Potential causes of opportunity loss in milk were inadequate diet from low availability and poor quality of forage, insufficient reserves of body tissues to support early lactation, and inadequate health management. Extending the results from other studies to this Sicilian case, where genetic parameters of dairy production have not yet been estimated, the unequal input use (environmental opportunity) associated with abnormal lactation would be expected to underwrite significant G×E in dairy performance.

Therefore, the objectives of this study were to evaluate potential G×E in yields of milk, fat and protein, and in somatic cell scores of Friesian and Brown Swiss cows by comparing genetic parameters and expected correlated responses in contrasting Sicilian herd environments alternatively defined. Farmers need to know the opportunity losses in daughter response due to management inputs, which are known to influence selection decisions (Holmann et al., 1990; Blake, 1992).

MATERIALS AND METHODS

Data and Edits

Mature equivalent (**ME**) lactation yields of milk, fat and protein and pedigree files were provided by the Italian Friesian Association (Associazione Nazionale Frisona Italiana) and the Italian Brown Swiss Association (Associazione Nazionale Allevatori Razza Bruna). Initial data comprising 39,030 records from 16,259 Friesian cows and 8685 records from 3430 Brown Swiss cows calving from January 1994 to December 1999 were edited for redundant and incomplete observations, lactations initiated by abortion, missing cow identification, pedigree errors, incorrect or inconsistent lactation number, age and date of calving and calving interval. Primiparous cows were 18 to 45 mo of age at calving. Herds with less than three records per herd-year and sires with less than two daughters were discarded. The final data for genetic analysis contained 8897 primiparous daughters of 825 Friesian sires and 1143 primiparous daughters of 220 Brown Swiss sires.

Test day milk yields and somatic cell counts of the first three lactations were provided by CoRFiLaC, Sicily's main dairy research center, and the Associazione Provinciale Allevatori of Ragusa, Sicily. At least four test day records were required per lactation. Observations for DIM less than 5 or greater than 310 and intervals less than 15 d or greater than 75 d between observations were not considered. Weighted SCS (WSCS) per lactation was created from the monthly somatic cell scores for each cow with at least one SCC. SCS, which is homoscedastic among samples, was calculated for each SCC observation as: $(\log_e SCC/\log_e 2)-(\log_e 12.5/\log_e 2)+12$. Because SCC is inversely related to daily milk yield (Jones et al., 1984), the WSCS was calculated using test day milk (m_i) associated with SCS as a weighting factor:

$$\mathrm{WSCS} = \frac{\sum_{i=1}^{n}(m_i SCS_i)}{\sum_{i=1}^{n} m_i}.$$

Data on management practices were from interviews with a special questionnaire (Raffrenato, 2002) of 168 Friesian and 71 Brown Swiss herd owners conducted in 2000 through CoRFiLaC. The survey included 82% of the Friesian and 86% of the Brown Swiss herds enrolled in the local dairy recording program (Associazione Provinciale Allevatori), the majority of the populations of herds for these breeds in Sicily's primary milk shed.

Definitions of Contrasting Herd Environments

Within herd-year standard deviation for lactation milk yield. The phenotypic HYSD for 305-day ME milk yield was used to discriminate herds like in other studies (Boldman and Freeman, 1990; Dong and Mao, 1990; Stanton et al., 1991a; 1991b; Cienfuegos-Rivas et al., 1999; Costa et al., 2000). Low opportunity environments had HYSD <1330 kg for Friesian herds and HYSD <950 kg for Brown Swiss herds. High opportunity environments were HYSD >1370 kg for Friesian herds and HYSD >990 kg for Brown Swiss herds. Accordingly, 132 Friesian herds and 37 Brown Swiss herds were allocated to the low HYSD class, and 76 Friesian and 30 Brown Swiss herds were allocated to the high class. There were 315 (of 825) Friesian sires and 63 (of 220) Brown Swiss sires with recorded daughters in both HYSD environments.

Detectable peak daily milk yield. Data files of test day milk records were obtained for cows in two parity groups: cows in first lactation and those in second and third lactations. The days in milk observations for these

records were divided into 31 classes for 18 age-at-calving groupings. The final data sets consisted of 195,705 records for 228 Friesian herds and 39,916 records for 78 Brown Swiss herds. Solutions were obtained with the following mathematical model for each DIM class for each parity group in each herd:

$$y_{ijklmn} = HYS_i + Age_j(H_k) + DIM_m(H_kP_l) + e_{ijklmn},$$

where y_{ijklmn} is the nth test day observation at herd-year-season i, age at calving class j, herd k, parity l and DIM class m; HYS_i is the level i for the herd-year-season fixed effect; $Age_j(H_k)$ is the level j of the fixed effect for age at calving nested within each herd; $DIM_m(H_kP_l)$ is the mth level of the fixed effect for DIM nested within herd and parity; and e_{ijklmn} is the random vector of residuals assumed to be normally distributed. Relationships among animals were ignored.

The DIM solutions for each herd and parity class were fit to an incomplete gamma function ($y = at^be^{-ct}$; Wood, 1967). Only cows with at least five test day records per lactation were analyzed. Herds permitting estimation for only one parity class were ignored to restrict classification errors. Detectable peak lactation was determined by testing the significance and sign of the b parameter using a significance threshold of $\alpha = 0.05$.

High opportunity Friesian herds were those with detectable peak lactation (i.e., b parameter value exceeded zero; $P < 0.05$) in primiparous and multiparous cows. Low opportunity Friesian herds were those with abnormal lactation in either parity group (i.e., b parameter value less than or not significantly different from zero). Low opportunity Brown Swiss herds were those with abnormal lactation in both parity groups, otherwise herds were assigned to the high environment. This response behavior would be expected to differentiate productive opportunity by nutritional and health inputs and orchestrated physiological, or homeorhetic, drivers of lactation. As a result there were 91 Friesian herds and 38 Brown Swiss herds in the low opportunity environment, and 136 Friesian and 38 Brown Swiss herds in the high environment. Similar proportions of herds were sought in the contrasted environments to assure sire representation and genetic ties between them.

Management practices that enhance milk production. Interviews of owners indicated there were no important changes in herd management across the time period covered by the lactation performance data. Therefore, survey responses to 17 questions about management inputs (Table 1) were used to form environmental clusters with contrasting input use frequencies. Input categories included nutrition management, milking practices, health practices, and animal handling.

Table 1. Survey questions about input use to discriminate herd productive opportunities.

Category
Nutrition management
Chemical analysis of forages
Feeding groups
Total mixed rations fed to lactating cows
Mineral supplementation for lactating cows
Milking practices
Individual towels to dry udders before milking
Teats dried after pre-dip or washing
Fore stripping before milking
Screening for abnormal milk
Post-milking teat disinfection
Equipment washed with detergent after each milking
Health practices
Antibiotic dry cow treatment
Antibiotic treatment of clinical mastitis
Farm visited at least monthly by veterinarian
Record-keeping system
Animal handling
Isolation of sick cows
Calves separated from dams at birth
Calves reared individually

Each practice was assigned an asymmetric binary value (0 = no, 1 = yes) whether it would be expected to enhance milking performance. The management environmental distance of Jaccard (Kuo, 1997) between two farms, x and y, was calculated as

$$d(x,y) = \frac{\sum_{i=1}^{n}\delta_{x,y}^i}{\sum_{i=1}^{n}\upsilon_{x,y}^i + \sum_{i=1}^{n}\delta_{x,y}^i}$$

where n = total number of questions considered, $\delta_{x,y} = 1$ if $x_i \neq y_i$, $\delta_{x,y} = 0$ otherwise and $v_{x,y} = 1$ if $x_i = y_i$, $v_{x,y} = 0$ otherwise. By this method a specified practice is weighted more than its absence. The resulting matrices of management distances between farms were used to form two groups of herds in each breed using the flexible beta clustering method (Lance and Williams, 1967), where the value of beta governs the distance between points merged into a cluster. A beta value of -0.25 was used as recommended for conditions of variable response and widely spaced clusters (Milligan, 1989). In our case this hierarchical agglomeration method signified similar causality in each environment, or predisposing dietary adequacy, udder health and other conditions affecting yield response. This criterion resulted in 95 Friesian and 27 Brown Swiss herds in the low environment, and 73 Friesian and 44 Brown Swiss herds in the high environment.

Some herds were classified as providing the same general opportunity with our definitions. For example, there were 68 Friesian herds and 22 Brown Swiss herds

common to the low HYSD and abnormal lactation environments; and 37 Friesian and 16 Brown Swiss herds with abnormal lactation and infrequent use of yield-enhancing practices. This set of criteria identified the same 25 (37) Friesian herds and 8 (6) Brown Swiss herds common to the low (high) environments.

Within-Environment Analysis

The components of variance and covariance and genetic parameters for first-lactation yields of milk, fat and protein, and weighted somatic cell score in each breed were estimated using a multiple-trait linear mixed sire model with unequal design matrices and a missing observations structure. All traits were analyzed for the average herd (all data) and low and high opportunity environments.

The model in matrix notation was:

$$Y = Xh + ZQg + Zs + e,$$

where Y = vector of records of traits within an environment; h = fixed herd-year-season effects; X = incidence matrix relating herd-year-season to records; ZQ = incidence matrix relating group of sires to daughters' records; g = fixed genetic group effects; Z = incidence matrix relating sires to daughters' records; s = vector of random sire effects; and e = vector of random errors. Assumptions were:

$$E(Y) = Xh + ZQg$$
$$E(s) = E(e) = 0$$
$$V(e) = I\sigma_e^2 = R_o \otimes I = R$$
$$V(s) = 0.25\sigma_s^2 \otimes A = G_o$$
$$Cov\ (s,\ e) = 0,$$

where $\otimes$ = refers to the Kronecker product; G_o = the genetic variance-covariance matrix; R_o = the environmental variance-covariance matrix; $V(e)$ = the residual variance.

Between-Environment Analysis

Components of covariance and genetic correlations between environments were estimated for each trait in each breed using a two-trait linear mixed sire model with unequal design matrices. This model was the same as for the within-environment analysis with identical assumptions. The size of A for the respective breeds was the same for every analysis regardless of environmental definition.

Correlated Response and Genetic Trend

Coefficients of correlated response in low opportunity environments from sire selection in the high opportu-

nity environment were estimated by genetic regression $\hat{\sigma}_{ij}/\hat{\sigma}_j^2$, where $\hat{\sigma}_{ij}$ is the estimate of sire covariance for pairs of traits in the contrasting environments and $\hat{\sigma}_j^2$ is the estimate of sire variance in the high opportunity herds.

Genetic trends in contrasting environments were estimated for each trait and breed by regression of the weighted (by number of daughters per sire) average sire predicted transmitting ability (PTA) on year of birth of their progeny. These PTA were obtained from the between-environment analysis by adding sire solutions from the mixed model equation to respective group solutions in the same system of equations. Average PTA was expressed as a deviation from the mean PTA of cows born in 1991.

RESULTS AND DISCUSSION

Low and High Opportunity Environments

Table 2 contains descriptive statistics for average herds (all data) and HYSD environments for Friesian and Brown Swiss cows. The HYSD definition of contrasting environments excluded 20 Friesian and 11 Brown Swiss herds to restrict overlap between them. One Friesian herd and two Brown Swiss herds were excluded for missing information to determine peak lactation. Sixty Friesian and seven Brown Swiss herds could not be clustered by management practices because they were no longer operating at the time of the survey.

Within-Environment Analysis

Yields of milk, fat, and protein. Components of covariance for yields of milk in contrasted environments are in Table 3 for Friesian cows and in Table 4 for Brown Swiss cows. Sire and residual variances were smaller in low than in high opportunity environments of both breeds. This compression of variance was like that observed in diverse situations in North America and Latin America (Castillo et al., 2000; Costa et al., 2000; Cienfuegos-Rivas et al., 1999; Dong and Mao, 1990; Meinert et al., 1988; Stanton et al., 1991b). The resulting heritabilities ranged from 0.21 to 0.28 in the two breeds, which, like the associated correlations (Raffrenato, 2002), were similar to other published estimates (Castillo et al., 2000; Costa et al. 2000; DeJager et al., 1987; Maijala et al., 1974; Manfredi et al., 1984; Roman and Wilcox, 2000; Seykora and McDaniel, 1983; Schutz et al., 1990; Welper et al., 1992). Unfortunately, components of covariance from a national study of Italian Friesian (Burnside et al., 1992) were not published, which precluded comparison with our results.

Table 2. Numbers of records, herds and sires, and means and standard deviations for mature equivalent (ME) yields of milk, fat and protein, and weighted somatic cell score for the average herd (mean of all data) and for low and high herd-year standard deviation (HYSD) environments for Friesian and Brown Swiss cows.

	Friesian[1]			Brown Swiss[2]		
	Average	Low	High	Average	Low	High
Records	8897	3753	4532	1143	467	556
Herds	228	132	76	78	37	30
Mean number of records/herd	39	28	59	14	11	18
Mean number of sires/herd	4	4	7	3	3	4
Sires	825	521	557	220	125	125
Mean daughters/sire	11	7	8	5	4	4
ME milk yield	9151	8368	9854	6889	6488	7246
Standard deviation	2078	1745	2137	1537	1328	1688
ME fat yield	308	283	330	255	237	270
Standard deviation	72	61	75	57	47	62
ME protein yield	277	251	300	231	216	244
Standard deviation	63	53	64	52	44	56
Score	3.31	3.33	3.30	3.22	3.47	3.01
Standard deviation	1.24	1.22	1.26	1.16	1.23	1.09
HYSD	1373	1118	1653	1016	875	1160

[1]HYSD classes: low <1330 kg, high >1370 kg milk.

[2]HYSD classes: low <950 kg, high >990 kg milk.

Variance component estimates for environments defined by incidence of abnormal lactation or differential use of milk yield-enhancing management practices were similar to the findings from HYSD definitions. Thus, a consistent compression of genetic variance was apparent in low opportunity herds regardless of environmental definition, but not in the associated heritability estimates (Raffrenato, 2002) due to disproportional changes in residual variances, which agrees with other studies (Boldman and Freeman, 1990; Carvalheira et al., 1998; Cienfuegos-Rivas et al., 1999; Costa et al., 2000; Dong and Mao, 1990; De Veer and Van

Table 3. Sire genetic and residual components of covariance for mature equivalent yields of milk, fat, and protein (kg^2), and weighted average somatic cell score for contrasted Friesian herd environments defined by within herd-year standard deviation (HYSD[1]), incidence of abnormal lactation[2], and differential use of management inputs.

Trait[3]	Milk	Fat	Protein	Score	Milk	Fat	Protein	Score	Milk	Fat	Protein	Score	Variance component
	Low HYSD				Abnormal lactation				Infrequent use of inputs				
Milk	**78,505**	2139	2060	−0.09	**109,986**	2355	2498	−0.05	**83,695**	674	1594	0.16	Sire
	1,058,817	27,328	26,983	−97.19	1,013,328	28,367	26,739	−99.27	1,908,029	50,843	51,338	−133.36	Residual
Fat		**123**	73	0.44		**63**	50	0.63		**110**	45	0.51	Sire
		1321	827	−3.50		1275	861	−4.33		2507	1539	−4.45	Residual
Protein			**76**	0.18			**69**	0.04			**57**	0.28	Sire
			826	−1.90			813	−1.65			1591	−2.75	Residual
Score				**0.03**				**0.03**				**0.05**	Sire
				1.06				1.08				1.15	Residual
	High HYSD				Normal lactation				Frequent use of inputs				
Milk	**121,480**	1541	2831	−4.41	**118,838**	2317	3061	−0.44	**122,439**	2364	2635	0.13	Sire
	2,105,249	55,561	56,032	−106.67	1,778,799	46,431	47,059	−106.55	1,471,705	37,989	38,039	−93.57	Residual
Fat		**255**	64	−0.11		**177**	87	0.25		**118**	52	0.60	Sire
		2571	1644	−3.25		2192	1386	−3.62		1654	1098	−3.32	Residual
Protein			**88**	−0.27			**106**	0.26			**78**	−0.02	Sire
			1705	1.18			1441	−2.25			1137	−1.45	Residual
Score				**0.03**				**0.05**				**0.04**	Sire
				1.18				1.13				1.10	Residual

[1]Low opportunity = HYSD <1330 kg and high opportunity = HYSD >1370 kg of milk.

[2]Herds with evidence of peakless lactation for first lactation or older cows were assigned to the abnormal (low opportunity) class. The remaining herds were assigned to the normal lactation (high opportunity) class.

[3]Variances are on the diagonals (bold).

Table 4. Sire genetic and residual components of covariance for mature equivalent yields of milk, fat, and protein (kg^2), and weighted average somatic cell score for contrasted Brown Swiss herd environments defined by within herd–year standard deviation (HYSD[1]), incidence of abnormal lactation[2], and differential use of management inputs.

Trait[3]	Milk	Fat	Protein	Score	Milk	Fat	Protein	Score	Milk	Fat	Protein	Score	Variance component
	Low HYSD				Abnormal lactation				Infrequent use of inputs				
Milk	**59,689**	2024	1689	24.59	**82,469**	2792	1933	18.77	**45,835**	1742	1662	22.04	Sire
	756,847	24,203	22,985	−39.43	**713,317**	24,349	21,373	127.37	**845,052**	30,507	25,418	−61.91	Residual
Fat		**110**	55	0.65		**130**	78	0.85		**90**	60	0.74	Sire
		997	791	0.34		**1045**	785	−4.74		**1286**	983	−1.14	Residual
Protein			**52**	1.18			**55**	0.83			**61**	0.87	Sire
			778	0.70			**734**	−3.31			**867**	−0.89	Residual
Score				**0.05**				**0.02**				**0.02**	Sire
				1.02				**0.93**				**0.97**	Residual
	High HYSD				Normal lactation				Frequent use of inputs				
Milk	**90,151**	2717	3208	13.52	**73,247**	2781	2690	13.15	**71,876**	1893	1688	29.34	Sire
	915,070	30,577	27,259	−50.23	**976,855**	31,679	29,806	−143.07	**909,516**	27,275	26,827	−47.13	Residual
Fat		**106**	102	−0.01		**136**	115	0.01		**94**	49	0.46	Sire
		1287	989	−2.50		**1296**	1,031	−2.63		**1062**	886	−3.33	Residual
Protein			**105**	0.01			**113**	0.29			**44**	0.41	Sire
			1102	0.97			**1010**	−3.37			**898**	−0.86	Residual
Score				**0.02**				**0.06**				**0.02**	Sire
				0.97				**0.93**				**0.85**	Residual

[1]Low opportunity = HYSD <950 kg and high opportunity = HYSD >990 kg of milk.

[2]Herds with evidence of peakless lactation for first lactation and older cows were assigned to the abnormal (low opportunity) class. The remaining herds were assigned to the normal lactation (high opportunity) class.

[3]Variances are on the diagonals (bold).

Vleck, 1987; Meinert et al., 1988; Short et al., 1990; Stanton et al., 1991b).

Weighted somatic cell score. Sire and residual covariances for weighted somatic cell score (Table 3) were similar between high and low Friesian environments, except for the possible smaller genetic variation with frequent abnormal lactation. Heritabilities in contrasting HYSD environments were 0.10 in both breeds (Raffrenato, 2002), which agreed with findings by Castillo-Juarez and co-workers (2000). Genetic correlations between score and yield traits were slightly favorable in high HYSD Friesian herds (range: −0.16 to −0.04), but they tended to be antagonistic in the low HYSD environments in both breeds (range: 0.02 to 0.42). Therefore, besides yield performance, genetic expression of weighted somatic cell score may also be affected in low opportunity environments.

Between-Environment Analysis

Multivariate analyses revealed important differences in genetic components of variance in differentiated environments. Therefore, estimates from bivariate analyses helped to further evaluate the expected impact of G×E on opportunity loss, or sacrifice, in genetic gain in the most restrictive environments. The resulting components of covariance for all definitions of low and high opportunity Friesian environments with heritabilities and genetic correlations for HYSD environments are in Table 5, and in Raffrenato (2002) for Brown Swiss herds.

HYSD environments. Sire variances for yield traits in both breeds were consistently smallest in the low opportunity environments, while estimates for somatic cell score were similar in the contrasted environments. Therefore, discussion focuses on results from the more plentiful Friesian data.

Sire and residual variance components for milk yield from low HYSD Friesian herds were about half as large as corresponding estimates from the high HYSD environment (Table 5). The genetic correlation (0.63) between these environments differed from unity ($P < 0.0001$) and was similar to the correlation in first-lactation milk yield between herds in the US and Mexico (Cienfuegos-Rivas et al., 1999), which suggests major re-ranking of sire breeding values. Components of variance for yields of fat and protein showed the same pattern. Genetic correlations between environments were 0.66 for fat and 0.48 for protein, both less than unity ($P < 0.0001$), also signaling substantial re-ranking in breeding values. Like the multivariate analysis sire and residual variances and the heritability of weighted somatic cell score (0.10) were similar in the contrasted environments.

Incidence of abnormal lactation. A similar pattern of response in yield traits was found, where genetic variation was less in herds with abnormal (peakless) lactation either in primiparous or pluriparous cows. Genetic varia-

Table 5. Estimates of sire and residual components of variance, sire covariance (Cov), heritability (h^2), and genetic correlation (r_g) for mature equivalent yields of milk, fat and protein, and weighted somatic cell score in contrasted environments of Friesian cows.

Trait	HYSD[1]			h^2	r_g	Lactation[2]			Management inputs		
	Sire	Residual	Cov			Sire	Residual	Cov	Sire	Residual	Cov
Milk, kg²											
Low	65,973	1,059,296	64,389	0.23	0.63[3]	65,326	1,015,389	80,428	98,092	1,913,604	104,861
High	156,047	2,108,799		0.27		99,021	1,811,951		128,186	1,468,661	
Fat, kg²											
Low	122	1324	113	0.33	0.66[3]	43	1263	82	202	2514	158
High	241	2585		0.34		156	1022		194	1637	
Protein, kg²											
Low	71	825	45	0.31	0.48[3]	92	799	96	100	1594	100
High	122	1710		0.26		101	1463		149	1120	
Score											
Low	0.029	1.059	0.028	0.10	0.96	0.036	1.081	0.03	0.023	1.154	0.024[3]
High	0.030	1.187		0.10		0.039	1.132		0.036	1.097	

[1] Within herd-year standard deviation (HYSD) classes: low opportunity <1330 kg and high opportunity >1370 kg milk.

[2] Herds with evidence of peakless lactation for first lactation or older cows were assigned to the abnormal (low opportunity) class. The remaining herds were assigned to the normal lactation (high opportunity) class.

[3] Genetic correlations between low and high opportunity environments differ from unity ($P < 0.05$).

tion was also compressed in low opportunity Brown Swiss herds (Raffrenato, 2002). These diminished responses may have been caused by too few nutritional and health inputs and disrupted homeorhetic pathways (physiological orchestration) in the early postpartum period. Genetic correlations between environments were large and positive (range: 0.95 to 0.99), indicating no important effect on the ranking of sire values. Sire variances for weighted somatic cell score were similar with no important change in breeding values indicated by the genetic correlations.

Differential management practices. As for other definitions of contrasting environments, the sire component of variance for milk yield was also smaller in Friesian herds where nutritional and udder health inputs and practices were used relatively infrequently. This finding is consistent with the result from multivariate analysis for this definition (Table 3). Less genetic variation also occurred in protein yield, but genetic variances were similar for yield of fat. Sire variances for yield traits of Brown Swiss cows also were least in the low input environment (Raffrenato, 2002).

Importantly, the sire variance for weighted somatic cell score in the low opportunity environment (both breeds) was less than in herds relying on more management (e.g., udder health). Consequently, the genetic correlation between environments differed from unity ($r_g = 0.83$, $P < 0.05$), indicating re-ranking in breeding values. Thus, differentiation of production environments based on our survey of management inputs and environmental clustering was effective in identifying heterogeneous genetic expression in these herds.

Overall, discriminating herd environments by any of these definitions, including the endogenous HYSD variable, revealed a consistent pattern of unequal genetic expression, or G×E, in yield traits. Furthermore, evidence was also found for G×E in weighted somatic cell score in both breeds. Collectively, this information indicates that the G×E occurring in about one-half of the dairy herds in Sicily's principal dairy region is mainly from compression in genetic expression fostered by input constraints.

Correlated Response and Genetic Trend

Compression in sire components of variance translates into diminished genetic gain from selection in low opportunity environments compared to herds with fewer limitations. The expected correlated responses in these environments for Friesian and Brown Swiss are in Table 6. Estimates generally indicate 20% to 60% less genetic gain in milking performance from indirect selection based on information from more privileged environments.

Table 6. Expected correlated responses in yields of milk, fat and protein, and weighted somatic cell score in the low opportunity environments as a proportion (genetic regression) of response in the high opportunity environments defined by herd-year standard deviation (HYSD), incidence of abnormal lactation, and differential use of yield-enhancing management inputs.

Environmental criterion	Milk	Fat	Protein	Score
		Friesian		
HYSD <1330 kg	0.41	0.46	0.36	0.93
Abnormal lactation	0.81	0.52	0.95	0.92
Infrequent use of inputs	0.81	0.81	0.67	0.66
		Brown Swiss		
HYSD <950 kg	0.75	0.53	0.43	0.68
Abnormal lactation	0.80	0.85	0.79	0.84
Infrequent use of inputs	0.67	0.86	0.82	0.61

Coefficients of expected correlated response for yield traits in the low HYSD environments for both breeds were smallest among our definitions. Sacrifices in yield response in these environments, relative to less constrained alternatives, were about one-half for Friesian and one-fourth to one-half for Brown Swiss. Less response was also predicted in herds with greatest abnormal (peakless) lactation and in herds with least frequent use of recommended nutrition, milking and udder health inputs (except protein yield in Friesian herds with abnormal lactation).

The expected correlated response in somatic cell score for both breeds was similarly depressed about 30% in herds with relatively little milk yield-enhancing management. This outcome may be due to less use of recommended udder health and milking practices. Coefficients for the other environmental definitions exceeded 0.80, except in low HYSD Brown Swiss herds.

Less sire variation in low opportunity environments reduced the expected selection response in both breeds, regardless of the definition. This result is consistent with findings from around the world (Boldman and Freeman, 1990; Carvalheira et al., 1998; Castillo-Juarez et al., 2000; Cienfuegos-Rivas et al., 1999; Costa et al., 2000; Dong and Mao, 1990; De Veer and Van Vleck, 1987; Meinert et al., 1988; Short et al., 1990; Stanton et al., 1991b) that unequal genetic progress and, thus, unequal net economic returns from genetic decisions are functions of identifiable input constraints. Net economic returns are depressed and optimal decisions are altered by diminished daughter milk response and predisposing environmental limitations (Blake, 1992; Holmann et al., 1990). Greater and more rapid genetic improvement in productivity and larger net economic payoffs would be expected by ameliorating the restrictions that foster G×E, including the ones in this study to identify low opportunity herds.

Figure 1 shows genetic trends for milk yield for Friesian (panels a and b) and Brown Swiss (panels c and d) in the contrasting environments defined by incidence of abnormal lactation and the use frequency of management inputs to increase milk yield. Genetic trends in herds with frequent abnormal lactation were inferior to those in environments with normal lactation, undoubtedly due to less expression of genetic variation in these herds. Annual trends with low inputs were mostly smaller than in less constrained environments.

The estimated average annual genetic gain was 20 kg milk for Friesian cows born from 1991 to 1997. This was similar to the 24 kg/yr gain in Brazilian Holstein (Costa et al., 1998), but inferior to gains of 57 kg/yr (1974 to 1984) and 173 kg/yr (1985 to 1988) reported in average Italian Friesian herds (Burnside et al., 1992). The sire components of variance for Brown Swiss yield traits in our study averaged 50% less than estimates from a sire-maternal grandsire model applied to the Italian Brown Swiss population (Santus et al., 1993), which resulted in 8 kg annual genetic gain in milk. Smaller variances and genetic gain in southeastern Sicily may have resulted from fewer management inputs than in average Italian herds in both breeds.

Positive genetic trends in alternative environments in both breeds indicated farmers' attention to sire selection. The differences between environments in annual genetic change for yield traits were consistently positive across criteria, which demonstrate the greater returns from selection that accrue in the more favorable environments. Annual genetic gain in weighted somatic cell score was positive but close to zero in every environmental definition.

CONCLUSIONS

A set of definitions of contrasting herd environments was applied to study genetic expression in yields of milk and milk components and weighted somatic cell score of Friesian and Brown Swiss cows in the principal dairy region of Sicily. The HYSD definition was a proxy for herd management, assuming that more effective management begets greater performance variability within a herd. Unfortunately, this criterion utilizes an endogenous variable potentially correlated with milk yield response (i.e., the "outcome"), which can potentially bias the resulting inferences. The incidence of abnormal lactation contains much less of this potential bias because fewer test days are required to detect ascent to a maximum daily milk yield, itself a management-responsive biological input to overall performance. Differentiated sets of management-clustered herds relied on exogenous information about input use to discriminate productive opportunities in a manner independent of the data (i.e., outcomes).

These definitions revealed consistent unequal responses in contrasting high and low opportunity environ-
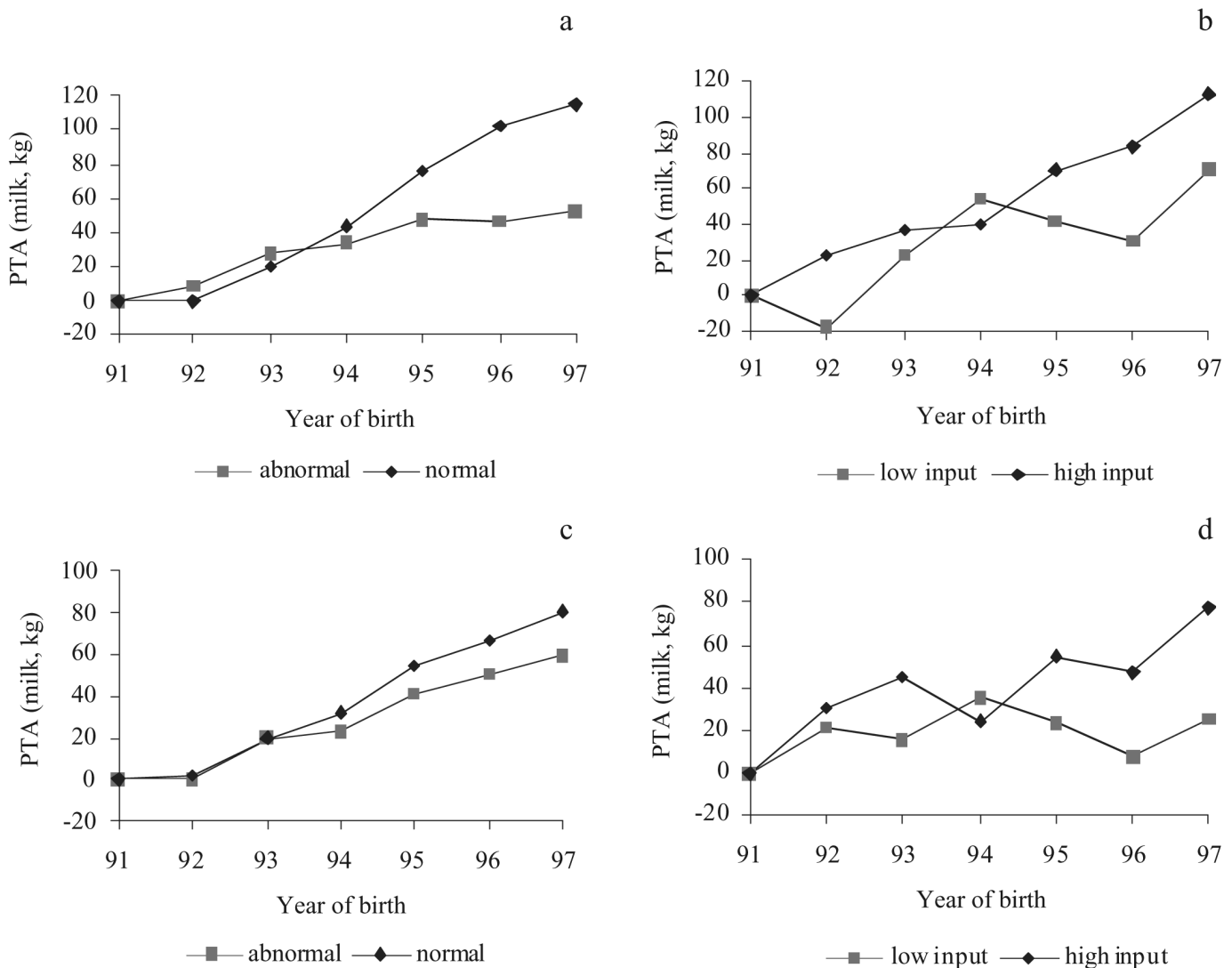
Figure 1. Genetic trend in average predicted transmitting ability (PTA) for milk of Friesian (a and b) and Brown Swiss (c and d) sires weighted by number of daughters in herds differing by frequency of abnormal lactation and use frequency of management inputs.

ments. Sire and residual variances for all traits were typically smaller in the low opportunity environments for within- and between-environment analyses. Heritability estimates for yield traits and for somatic cell score with these definitions were similar to those from previous reports. In general, genetic correlations were less favorable in the low opportunity environments. Antagonistic genetic correlations between yield traits and somatic cell score may have been attenuated by greater inputs in the high opportunity herds.

Except for the HYSD definition, genetic correlations between contrasted environments were near unity for yields of milk, fat and protein, indicating similar genetic controls. However, as in other studies relying on endogenous definition, compressed variance in breeding values

(i.e., scaling effect) rather than change in rank was the key evidence for G×E. The expected correlated responses in yield traits were about 40% less in low opportunity herds when selection was based on information from more privileged environments. Furthermore, small correlated responses in somatic cell score in both breeds were detected in environments with infrequent use of preferred management, including udder health and milking procedure. This is additional evidence for environmental restriction of genetic expression (variation), which signifies less gain from selection regardless of specific selection goals.

Ideally, it would be best to cluster herds using exogenous information, as in this study. Nonetheless, findings clearly showed that the consequences are not severe

when using HYSD to differentiate environments. Contrasting environments defined by the incidence of peakless lactation has potential advantages because nutritional and health inputs and homeorhetic mechanisms control or predispose this behavior. An appealing alternative, because it would be easy to implement, would be to depict herd responses as a continuous environmental gradient (reaction norm) of normal and peakless lactation curves using *b* parameter solutions (or their lower confidence limits) from the incomplete gamma function.

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