

## Genotype by Environment Interaction for Milk Production Traits Between Organic and Conventional Dairy Cattle Production in The Netherlands

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### ABSTRACT

Estimates of genetic parameters for organic dairy farming have not been published previously, and neither is information available on the magnitude of genotype by environment interaction (G×E) between organic and conventional farming. However, organic farming is growing worldwide and basic information about genetic parameters is needed for future breeding strategies for organic dairy farming. The goal of this study was to estimate heritabilities of milk production traits under organic farming conditions and to estimate the magnitude of G×E between organic and conventional dairy farming. For this purpose, production records of first-parity Holstein heifers were used. Heritabilities of milk, fat and protein yield, and somatic cell score (SCS) were higher under organic farming conditions. For percentages of fat and protein, heritabilities of organic and conventional production were very similar. Genetic correlations between preorganic and organic, and organic and conventional milk production were 0.79 and 0.80, respectively. For fat yield, these correlations were 0.86 and 0.88, and for protein yield, these were 0.78 and 0.71, respectively. Our findings indicate that moderate G×E was present for yield traits. For percentage of fat and protein and SCS, genetic correlations between organic and conventional and preorganic production were close to unity, indicating that there was no G×E for these traits.

**Key words:** genotype by environment interaction, organic dairy production, somatic cell score

### INTRODUCTION

Organic farming in Europe has developed into a small (about 3% of total agricultural area) but important factor in agricultural production (Organic Centre of Wales, 2005). In the Netherlands, organic dairy farming grew

rapidly in the late 1990s. Farmers who converted to organic production had to undergo some major changes in their farm management. The most important changes were no use of chemical fertilizers, restricted use of concentrates (cattle diets should have a minimum of 60% DM from conserved or fresh forage), and limited use of antibiotics (prophylactic use of antibiotics and some other drugs is prohibited on a herd basis; European Union, 1999).

Consequently, cows in organic farming have a lower intake of energy and protein and antibiotics are only administered in case of severe infections. The change in feed has the greatest effect on high-producing cows (Padel, 2000), usually Holsteins. Most organic dairy farmers in the Netherlands milk Holstein cows (Nauta et al., 2001). Significant changes in milk production have been observed at these farms and SCS have increased significantly since conversion (Nauta et al., 2006).

In this organic environment, dairy farmers have continued to use the same breeding bulls supplied by AI companies as their conventional colleagues (Nauta et al., 2001). European Union legislation currently gives few specific guidelines for selective breeding other than farmers must account for the “capacity of animals to adapt to local conditions, their vitality and disease resistance” and that indigenous breeds are preferred (European Union, 1999). However, Dutch farmers mainly use Holstein cattle, which have a high genetic potential for production. Increasingly, questions are being raised by farmers and researchers about the use of highly productive animals under organic conditions. There are indications that such animals cannot cope with the organic environment (Hardarson, 2001; Nauta et al., 2001), which raises the question whether organic dairy production needs a specific selection program for breeding bulls.

At this time, it is not clear whether organic dairy production requires specific selective breeding programs distinct from programs for conventional production. An important parameter to consider is the magnitude of genotype by environment interaction (G×E),

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which occurs when different genotypes react differently to different environments (Falconer, 1989).

At present, no information is available on the magnitude of a possible G×E between organic and conventional production. The existence of G×E might lead to a reranking of bulls and might have consequences for the organic farmer's choice of genetic material. A useful way to quantify G×E is the genetic correlation between traits as expressed in 2 environments (Falconer, 1989).

Environmental changes can also cause changes in phenotypic and genotypic variances of traits and differences in heritability may occur (Brotherstone and Hill, 1986). There is no information available about these parameters for organic dairy production.

The aim of this study was to estimate the heritabilities of different milk production traits including SCS for organic dairy farming and to quantify the magnitude of G×E between organic and conventional dairy production.

## MATERIALS AND METHODS

### Data

First-parity 305-d lactation records of Holstein cows from organic and conventional farms in the Netherlands were used in the present study. The data was from calvings between January 1990 and March 2004. The data were selected as described by Nauta et al. (2006). In brief, only records of cows that calved between 17 and 36 mo of age were included in the analysis. Days open were days between calving and last insemination and only records of cows with days open between 30 and 250 d were included. Records of cows that switched during the lactation from one farm to another were excluded from the analysis. Only 305-d records predicted based on more than 180 d in lactation were used.

The data set consisted of 188 organic farms; i.e., farms that converted to organic farming between 1990 and 2002, and 152 conventional farms. Conventional farms were randomly selected from all conventional farms located in the same postal areas as the organic farms. Lactation records before conversion were also available from the organic farms. Based on the date of conversion of each organic farm, the data from organic farms were divided into 3 environmental groups: 1) Preorganic: data from lactations belonging to calving dates from at least 9 mo before the date of conversion; 2) Converting-to-organic: data from lactations between 9 mo before the conversion date until 2 yr after the conversion date; and 3) Organic: data 2 yr after conversion and onwards.

By defining preorganic as records from at least 9 mo before conversion, we avoided having records of lactations that were partly under organic conditions. Definition of groups was based on the findings that the milk

production level started to decline about 1 yr before conversion and stabilized 2 yr after conversion to organic farming (Nauta et al., 2006). After initial edits, 21,364 first-lactation records from organic farms were available with 11,028 records from the preorganic period, 5,518 records from the converting-to-organic period, and 4,818 records from the organic period. The conventional data set consisted of 21,138 first-lactation records. Additional restrictions were that herd-year-season (HYS) classes should have at least 4 observations and each sire should have at least 4 daughters in the complete data set; that is, the combined organic and conventional data sets. An overview of the data is given in Figure 1 and Table 1.

The average SCS per lactation were based on SCC from test-day records. Only SCS were used of lactations with at least 5 and no more than 12 test days. Firstly, the SCC per test day were transformed to SCS using the formula:  $SCS = \log_{10}(SCC/1,000)$ . The average SCS per lactation was estimated as the mean of the test-day SCS per lactation. Not all cows with milk production records had records for SCS. Records with an SCS were also edited to get at least 4 records per HYS class and per sire. After the edits, pedigree information was traced back 5 generations and was included in the analysis.

Genetic connectedness between the different environmental groups is illustrated in Table 2, which shows the number of bulls in each environmental group as well as the number of bulls that had daughters in one group as well as in another.

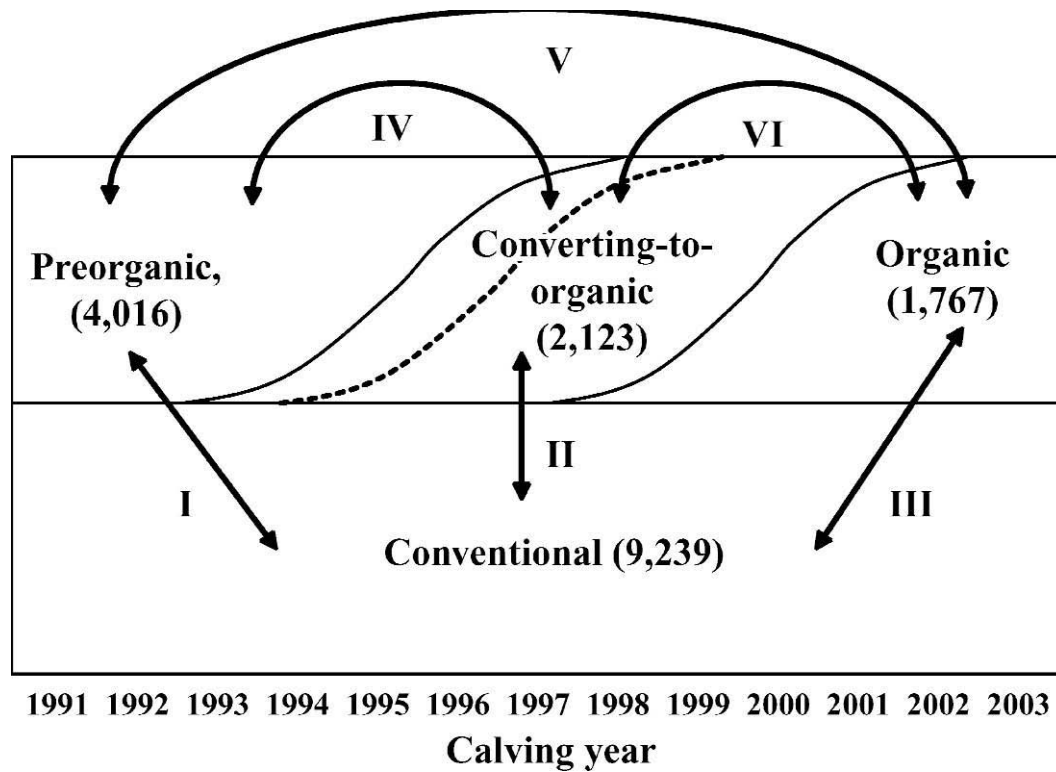
Heritabilities of milk production traits for each defined group and correlations between the different groups for milk yield, fat yield, protein yield, fat and protein percentages, and SCS were analyzed using AS-REML (Gilmour et al., 1999). The 4 groups were analyzed simultaneously in a multivariate analysis; that is, a trait recorded on animals in each of the groups was considered as a different trait.

### Model for Analyses

The model used was:

$$Y_{ij} = \mu + HYS_i + \beta_1 \times AFC_{ij} + \beta_2 \times (AFC_{ij})^2 + \beta_3 \times DO_{ij} + \beta_4 \times (DO_{ij})^2 + Animal_{ij} + e_{ij} \quad [1]$$

where  $Y_{ij}$  = observation on animal  $j$ ;  $\mu$  = overall mean;  $HYS_i$  = fixed effect of herd-year-season of calving  $i$ , the HYS effect was based on 4 seasons; January–March, April–June, July–September, and October–December;  $AFC_{ij}$  = covariable of age at first calving for observation  $ij$  (in mo);  $DO_{ij}$  = covariable of days open for observation



**Figure 1.** Schematic overview of the data and estimated genetic correlations (arrows I to VI). The lower part of the figure represents the data from conventional farms between January 1990 and March 2003. The upper part (preorganic + converting + organic) is from farms that converted to organic farming between 1990 and 2003 and were all organic in 2002. The dotted sigmoid curve reflects the dates of conversion to organic of the farms. Number of records per environmental group is shown in parentheses.

$ij$  (between calving and new conception);  $\beta_1$  to  $\beta_4$  = regression coefficients for linear and quadratic regression on age at calving in months ( $\beta_1$  and  $\beta_2$ ) and days open ( $\beta_3$  and  $\beta_4$ );  $Animal_j$  = random additive genetic effect of animal  $j$ ; and  $e_{ij}$  residual.

Random animal effects were assumed to be normally distributed with mean zero and variance  $A\sigma_A^2$ , where  $A$

is the additive genetic relationship matrix. The residual terms were assumed to be normally and independently distributed with mean zero.

In the multivariate analysis, 6 different genetic correlations were estimated simultaneously. This is schematically illustrated in Figure 1. Preliminary, bivariate analyses were performed for every combination of envi-

**Table 1.** Number of herds and records, and mean ( $\pm$ SD) values of milk production traits and SCS of the 4 environmental groups

	Environmental group			
	Conventional	Preorganic	Converting-to-organic	Organic
No. of herds	152	138 <sup>1</sup>	135 <sup>1</sup>	109 <sup>1</sup>
No. of records	9,239	4,016	2,123	1,767
Milk, kg	7,156 (1,203)	6,991 (1,219)	6,622 (1,145)	6,440 (1,158)
Fat, kg	310 (48.6)	299 (49.5)	284 (49.5)	274 (48.9)
Protein, kg	246 (39.1)	240 (40.7)	223 (38.6)	214 (38.1)
Fat, %	4.36 (0.46)	4.32 (0.45)	4.31 (0.45)	4.29 (0.46)
Protein, %	3.45 (0.19)	3.44 (0.20)	3.37 (0.20)	3.34 (0.19)
No. of SCS records	5,193	2,316	1,457	1,120
SCS	1.77 (0.34)	1.75 (0.34)	1.79 (0.33)	1.84 (0.31)

<sup>1</sup>Some of the herds appear in more than 1 of the 3 organic environmental groups. The organic group data comprised 188 farms that converted to organic farming between 1990 and 2002.

**Table 2.** The number of bulls with daughters in each of the 4 environmental groups and the number of bulls with daughters in one as well as in another group, which reflects the connectedness between data sets<sup>1</sup>

	Conventional	Preorganic	Converting-to-organic	Organic
Conventional	543	294	253	202
Preorganic		346	170	91
Converting-to-organic			291	153
Organic				237

<sup>1</sup>The total number of bulls in all groups was 634.

ronmental groups (results not shown). Bivariate analysis that resulted in estimated correlations close to unity were fixed in the multivariate analysis at a value of 0.999.

To test the significance of G×E between conventional and organic farming conditions, the likelihood ratio test was used. Genotype by environment interaction is reflected by the genetic correlations between preorganic and organic and between conventional and organic. Therefore, the log likelihood of a full model was compared with the log likelihood of a model in which the genetic correlations between conventional and organic and between preorganic and organic were fixed at unity. A  $\chi^2$  test with 2 degrees of freedom was used to test for the significance of G×E.

## RESULTS

### Variances and Heritabilities

Table 1 shows that milk, fat, and protein yields were about 10% lower in organic farms compared with conventional farms. The standard deviation for milk yield

tended to be slightly lower under organic farming conditions compared with conventional farming. However, the coefficient of variation was slightly higher for organic farms than for conventional farms (18.0 vs. 16.8%, respectively). Compared with conventional production, fat and protein yields per first lactation in organic farming were 36 and 23 kg lower, respectively. The coefficient of variation of both traits was higher in organic farming compared with conventional farming (17.8 vs. 15.8%). Compared with conventional production, fat and protein percentages in organic production were 0.07 and 0.11% lower, respectively. Their coefficients of variation were very similar.

A total of 5,193 production records of conventional farms and 4,893 production records of organic farms had a record of SCS. The SCS in organic production was 0.07 points higher than in conventional production and the coefficient of variation of SCS was lower in organic production (16.8 vs. 19.2%).

The estimated phenotypic variances ( $\sigma_p^2$ ), i.e., after adjusting for the fixed effects in the model, were lower in the organic environment than in the conventional

**Table 3.** Estimates of phenotypic variances ( $\sigma_p^2$ ) and heritabilities ( $h^2$ , SE in parentheses) of milk production traits and SCS of the conventional, preorganic, converting-to-organic, and organic production environments<sup>1</sup>

		Conventional	Preorganic	Converting	Organic
Milk yield	$\sigma_p^2$	871,190	839,087	735,170	734,014
	$h^2$	0.48 (0.03)	0.39 (0.04)	0.59 (0.07)	0.70 (0.08)
Fat yield	$\sigma_p^2$	1,411	1,359	1,174	1,138
	$h^2$	0.39 (0.03)	0.37 (0.05)	0.44 (0.07)	0.58 (0.08)
Protein yield	$\sigma_p^2$	786	762	651	663
	$h^2$	0.39 (0.03)	0.31 (0.04)	0.45 (0.07)	0.59 (0.09)
Fat, <sup>1</sup> %	$\sigma_p^2$	0.202	0.195	0.184	0.187
	$h^2$	0.79 (0.03)	0.83 (0.03)	0.82(0.05)	0.79 (0.06)
Protein, %	$\sigma_p^2$	0.035	0.033	0.033	0.031
	$h^2$	0.72 (0.03)	0.76 (0.04)	0.77 (0.06)	0.70 (0.07)
SCS	$\sigma_p^2$	0.099	0.094	0.098	0.099
	$h^2$	0.15 (0.03)	0.28 (0.06)	0.15 (0.06)	0.23 (0.08)

<sup>1</sup>Estimates obtained from bivariate analyses of percentage fat whereas multivariate analyses were fixed at boundaries and no standard errors could be estimated.

and preorganic environment groups (Table 3). Similar differences were found for fat and protein yields. The heritability of milk yield was 0.48 for conventional farms and 0.70 for organic farms. The heritabilities of fat and protein yield in conventional farming were 0.39 for both traits, whereas these were 0.58 for fat yield and 0.59 for protein yield in the organic environment.

For fat and protein percentages, the phenotypic variances of conventional and organic farming were very similar. In conventional farming, the heritabilities were 0.79 for fat percentage and 0.72 for protein percentage, whereas for organic farming these heritabilities were 0.79 and 0.70, respectively.

For SCS, the phenotypic variances for all environmental groups were between 0.094 and 0.099. The heritability of SCS was 0.15 for conventional, 0.28 for preorganic, and 0.23 for organic production.

### **Connectedness and Genetic Correlations**

The lowest connectedness (19%) was found between the preorganic and organic groups (Table 2). The other percentages of connectedness ranged between 35 and 50%.

The bivariate analyses for milk and protein yield showed that the genetic correlations between conventional and preorganic production were equal to 1. In the multivariate analysis, therefore, the correlations were fixed at a value of 0.999 (Figure 2) for these traits. The bivariate analyses for fat yield showed that the genetic correlation between converting-to-organic and organic was equal to 1. Therefore, in the multivariate analysis, this correlation was also fixed at a value of 0.999. For fat and protein percentages, the bivariate analyses showed that 4 of the 6 correlations were very close to unity. These correlations were fixed at 0.999 in the multivariate analyses of fat and protein percentage. For fat percentage, it was necessary to fix the other 2 correlations to let this analysis converge. These correlations were therefore fixed at the values 0.946 and 0.973, which were obtained in the bivariate analyses.

Multivariate analysis produced a genetic correlation of 0.80 between conventional and organic milk yield. Between preorganic and organic milk yield, the correlation was 0.79 (see Figure 2). The likelihood ratio test showed that, from a genetic point of view, milk yield under organic farming conditions was significantly different from milk yield under conventional conditions ( $P < 0.01$ ).

For fat yield, the genetic correlation between conventional and preorganic production was close to unity (0.97) and the genetic correlations between conventional and organic, and preorganic and organic were 0.88 and 0.86, respectively. The likelihood ratio test did

not give any evidence to support the assumption that fat yield under organic and conventional production circumstances were genetically different traits.

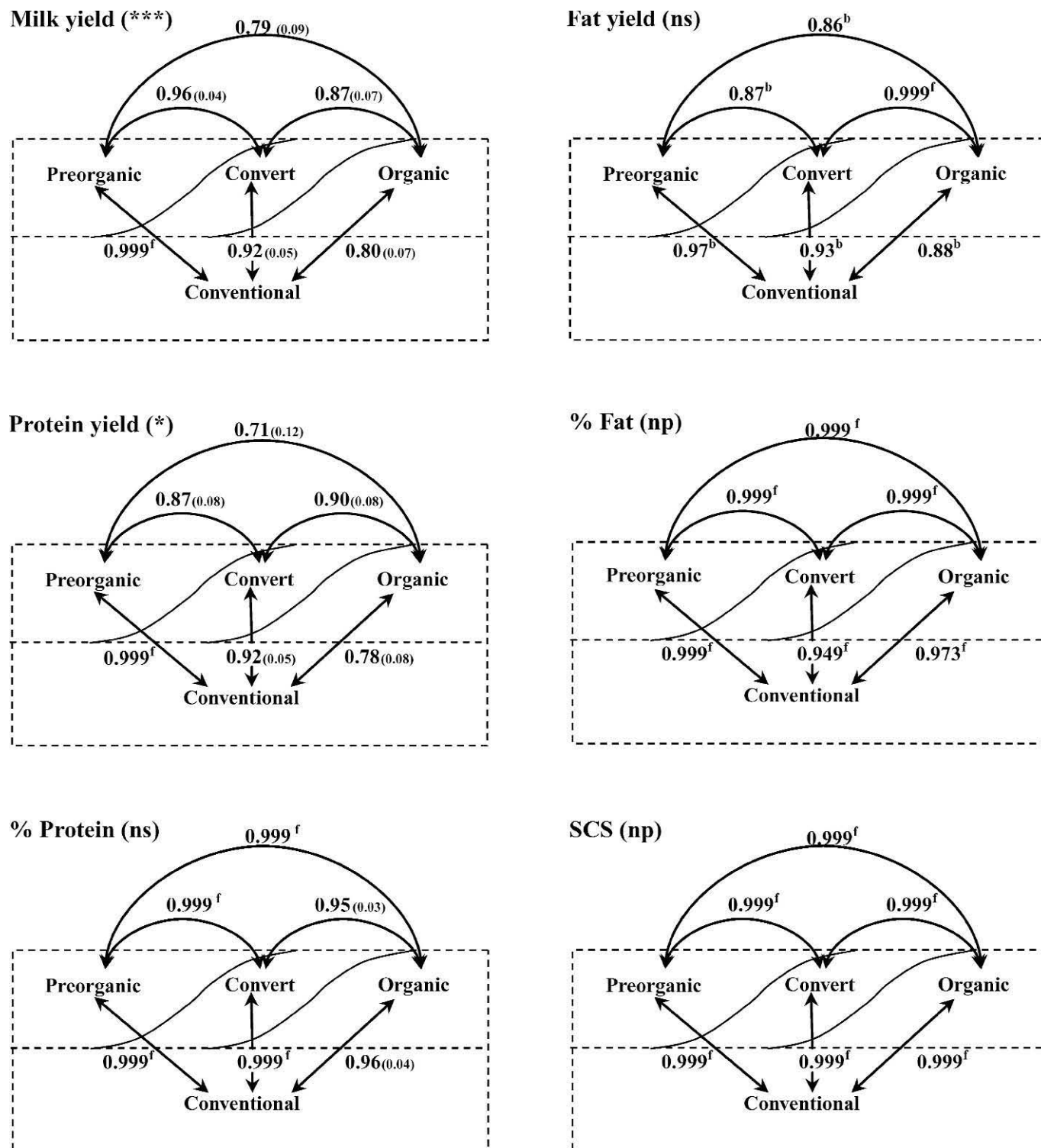
For protein yield, the genetic correlation between conventional and organic was 0.78, and between preorganic and organic production, 0.71. The correlations for protein yield were found to be significantly different from unity ( $P < 0.05$ ) showing that protein yield was different trait in organic production compared with conventional conditions. In the multivariate analyses, correlations could be estimated only for protein percentage. These correlations were close to unity and did not differ significantly from unity. The bivariate analyses showed that the genetic correlations for SCS were close to unity for all 6 combinations of environmental groups and therefore no likelihood ratio test was performed for this trait.

As a by-product of the genetic analysis, breeding values of all animals were estimated for the different traits. Ten bulls had at least 20 daughters in the conventional and organic groups, enabling the estimation of breeding values based on both environments. Figure 3 shows the estimated breeding values of these 10 breeding bulls for milk production in the conventional and organic environments. Distinct breeding values for conventional and organic farming resulted in a considerable reranking of bulls with respect to milk yield.

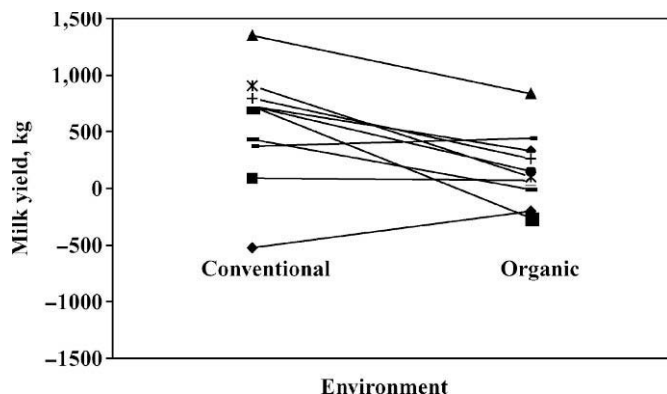
## **DISCUSSION**

### **Multivariate Analyses**

The present study combined 2 different ways of estimating genetic correlations between traits measured in different environments: 1) within farms, based on data from farms that switched from conventional to organic production and 2) between farms, based on data from organic farms and a random selection of conventional farms. The data obtained from farms that switched to organic farming were divided into 3 different farm environment groups: preorganic, converting-to-organic, and organic. The converting-to-organic group was introduced because a period of about 3 yr was observed in which milk production of cows decreased during conversion to organic production (Nauta et al., 2006). Estimated parameters for this group were of no particular interest, but the data were kept in the analysis because it provided genetic links between the preorganic and the organic group. Using multivariate analysis, all the evidence for the presence of G×E interaction could be combined: within farms switching from conventional to organic farming, as well as between conventional and organic farms.



**Figure 2.** Genetic correlations of milk production traits between the different farm environments. For description, see Figure 1. Significance was tested with a likelihood ratio test between the log likelihood of a full model and a model in which the genetic correlations between conventional and organic and between preorganic and organic were fixed at unity. A  $\chi^2$  test with 2 degrees of freedom was used to test for the significance of the genotype by environment interaction. <sup>f</sup> = correlation fixed, SE between brackets; \*\*\*  $P < 0.01$ ; \*  $P < 0.05$ ; ns = not significant; np = not performed.



**Figure 3.** Breeding values for milk yield of 10 bulls based on the environmental groups: conventional and organic. Each bull had at least 20 daughters in each environment.

### Phenotypic Variances and Heritabilities

Variances and heritabilities of yield traits of conventional production in this study were similar to other studies (e.g., Van Vleck and Van Dong, 1988; Van der Werf and de Boer, 1989). Surprisingly, the estimated heritabilities of yield traits in organic production circumstances were higher than in conventional production systems. The main reason for this was the residual variance ( $\sigma_e^2$ ) of yield traits, which was lower for organic farms. Also, the estimate for the additive genetic variance ( $\sigma_a^2$ ) of yield traits was higher under organic production circumstances than for conventional or preorganic production. In low-input production environments, production traits are generally found to have a lower heritability (Castillo-Juarez et al., 2002; Berry et al., 2003; Raffenato et al., 2003). Compared with conventional production, organic production can be considered a low-input production system: fewer concentrates are fed (W. J. Nauta, unpublished data) and organic roughage generally contains less energy (Plomp, 2003). Also, the use of veterinary drugs is limited in organic production, including a ban on preventive use of antibiotics for udder health (European Union, 1999).

When HYS classes were put in the model as fixed classes (instead of random), they explained a substantially larger part of the variation under organic farming conditions than under conventional conditions. The increased importance of HYS effects might reflect differences in management between organic farms, which could be caused by the fact that most organic farmers converted between 1998 and 2001 and were therefore relatively “young” organic farms still adjusting their management to the new organic situation (Østergaard, 1997).

Regarding the percentages of fat and protein, the variance components of conventional and organic pro-

duction agreed with other studies on conventional farming (Cue et al., 1987; Schutz et al., 1990; Campos et al., 1994). The heritability of these traits did not differ much between organic and conventional production.

The heritability of SCS in first-lactation heifers in conventional farming was higher than the heritability of SCS found in other studies (Schutz et al., 1990; Reents et al., 1995; Castillo-Juarez et al., 2000; Mulder et al., 2004). Banos and Shook (1990) found a similar heritability of SCS of 0.13 in first-parity Holstein heifers. The phenotypic variance of SCS in organic production was similar to conventional production, but due to a lower residual variance in organic production and a higher genetic variance of SCS, the heritability of SCS in organic production was 0.25. Castillo-Juarez et al. (2002) also found a higher heritability of SCS in a low-yield environment compared with a high-yield environment, but the difference was only 2%. A higher heritability of SCS in organic production could increase the possibilities for selecting for this trait within the organic production environment. However, standard errors of the heritability estimates of yield traits and SCS were considerable, especially for organic conditions.

### Genetic Correlations

The genetic correlation of about 0.80 for milk yield can result in a considerable reranking of bulls (Figure 3). However, Figure 3 shows only bulls that were used mostly by farmers and can therefore be considered as being top bulls. Reranking due to  $G \times E$  is more likely with high-ranking bulls (Mulder et al., 2004). It is also remarkable that there were so few bulls with at least 20 daughters in the data from organic production. Organic farmers probably use other breeding bulls than their conventional colleagues. It was recently found that organic farmers put more emphasis on functional traits (W. J. Nauta, unpublished data; P. Rozzi, OntarioBio, Guelph, ON, Canada, personal communication), which might be a reason for a different selection.

The genetic correlation between organic and conventional milk yield was low (0.80) compared with other studies on conventional production in the Netherlands (Ten Napel and Van der Werf, 1992; Calus et al., 2002; Mulder et al., 2004), in which genetic correlation was close to unity. The correlations in the present study between conventional and organic production for fat yield (0.86 to 0.88), and especially protein yield (0.71 to 0.77) correspond more with correlations found between New Zealand and North American and European countries, which were around 0.72 for milk yield (Interbull, 2003). Weigel et al. (2001) also found low genetic correlations (between 0.80 and 0.90) between rotational grazing systems and intensive management systems.

Low genetic correlations (0.48 to 0.66) were found between high- and low-opportunity environments for yield traits in Sicilian herds (Raffrenato et al., 2003); Berry et al. (2003) estimated a genetic correlation of 0.63 between high and low concentrate feeding level groups in Ireland.

The low correlations are thought to be due to differences in feeding level or feeding systems between the countries or farm environments. In New Zealand, dairy farming is primarily based on grazing and is therefore, to some extent, comparable with the Dutch organic dairy-farming sector, which is also more grass-based with lower concentrate inputs (Plomp, 2003; W. J. Nauta, unpublished data). The estimated correlations for milk yield traits in the present study were based on information from farms that converted to organic in the late 1990s. At that time, organic farmers could still feed relatively large quantities of concentrates, up to 1,800 kg per lactation (W. J. Nauta, unpublished data). Since August 2005, the European organic farmers are required to use concentrates that contain at least 95% organic ingredients (European Union, 1999). This will probably increase the cost of concentrate feeding, so that organic dairy production may resort increasingly to roughage. Genetic correlations between conventional and organic production might therefore decline further in the near future.

For SCS, it was not possible to make an estimation of genetic correlations, probably because all genetic correlations were close to unity as shown in the bivariate analyses.

When genetic correlations of traits decrease, the need for a separate breeding program increases (Mathur and Horst, 1994; Mulder and Bijma, 2005). In the current study, the estimated standard errors of the genetic correlations were high and definite conclusions cannot be drawn yet. However, with decreasing differences between organic and conventional production as mentioned above, the need for a separate breeding program for organic farming may grow. However, the organic dairy sector is still relatively small and farmers increasingly use a variety of different breeds and crossbreeds (W. J. Nauta, unpublished data). Currently, there are still about 10,000 Holstein dairy cows on organic farms in the Netherlands. Only a small number of bulls of this breed could be tested under organic conditions each year. It could be a start for organic-based cattle breeding, but the organic sector must still decide whether a separate breeding program is preferable or not.

## CONCLUSIONS

Heritabilities of production traits and SCS tended to be higher in organic than in conventional farming,

which creates possibilities for selection and genetic progress under organic production circumstances.

Based on the results of this first study, the magnitude of G×E between conventional and organic milk yield and fat and protein yield is of importance and comparable with G×E between a grass-based system as in New Zealand and high-input systems as in North America or Western Europe. The magnitude of G×E will result in a reranking of breeding bulls for organic milk and protein production, based on their breeding values for these traits. The magnitude of G×E will probably increase when restrictions on concentrate feeding are increased in the future, especially for high-yielding cows. When genetic correlations fall below 0.80, specific breeding values for organic dairy production with high-yielding cows become more important in making an adequate selection of breeding bulls for organic dairy production.

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