Effects of genotype by environment interaction on genetic gain in breeding programs

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ABSTRACT: Genotype by environment interaction (G × E) is increasingly important, because breeding programs tend to be more internationally oriented. The aim of this theoretical study was to investigate the effects of G × E on genetic gain in sib testing and progeny testing schemes. Loss of genetic gain due to G × E was predicted for different values of heritability, number of progeny per sire, and generation interval. Two environments were considered: a selection environment (SE) and a production environment (PE). The breeding goal contained only performance in PE. A pseudo-BLUP selection index was used to predict genetic gain.

Recording of half-sibs or progeny in PE limited the loss in genetic gain in PE due to G × E between SE and PE. Progeny testing schemes had a lower loss in genetic gain than sib testing schemes. Higher heritability increased the loss in genetic gain, whereas increasing the number of progeny per sire in PE decreased the loss in genetic gain. The required number of progeny per sire to minimize loss in genetic gain due to G × E was larger for sib testing schemes than for progeny testing schemes. It was concluded that recording performance of relatives in PE minimizes loss in genetic gain due to G × E and that progeny testing schemes are preferable in situations with low to moderate heritability ($h^2 \leq 0.3$), relative short generation interval of progeny tested sires ($L_{prog} / L_{sib} \leq 1.7$), and moderate to severe G × E interaction ($r_g \leq 0.8$).

INTRODUCTION

Livestock breeding programs are becoming more international, which means that their goal is to breed animals that can perform well in a variety of environments. As a consequence of internationalization of breeding programs, knowledge of the effects of genotype by environment interaction (G × E) on genetic gain in breeding programs is increasingly important. Due to G × E, genetic rank of animals might change, causing that the best animal in one environment might not be the best animal in another environment (Falconer and Mackay, 1996). The concept of genetic correlation between environments can be used as a measurement of ranking differences due to G × E (Falconer, 1952). In many situations estimates of the genetic correlation are lower than unity (Merks, 1988; Wei and Van der Werf, 1995; Weigel et al., 2001), indicating that selection of parents in one environment may decrease genetic gain of progeny performing in another environment.

Research has been carried out to optimize specific breeding programs of different species in the presence of G × E (e.g. Meuwissen and Woolliams, 1993; Bijma and Van Arendonk, 1998; Jiang and Groen; 1999). Based on these studies, however, it is difficult to identify the effects of G × E on genetic gain in combination with other parameters like heritability and number of progeny per sire. Furthermore, none of those studies compared sib testing and progeny testing schemes.

The objective of this study was to investigate the effects of G × E on genetic gain in sib testing and progeny testing schemes. Loss of genetic gain due to G × E was predicted for different values of heritability, number of progeny per sire, and generation interval. In the discussion strategies are discussed to minimize G × E or to deal with G × E in breeding schemes.

MATERIALS AND METHODS

Breeding schemes

In this study, two environments were considered: a selection environment (SE) with all selection candidates and a production environment (PE) with commercial animals, which were not used as selection candidates. Different degrees of G × E between SE and PE were created by varying the genetic correlation (Falconer, 1952). The breeding goal was performance in PE. Breeding schemes were either based on sib testing or progeny testing. Three breeding schemes were designed: (1) selection environment sib testing (SEsib), (2) combined selection environment and production environment sib testing (CSPsib) and (3) combined selection environment and production environment progeny testing (CSPprog). In SEsib and CSPsib, sires and dams were sib tested, whereas in CSPprog, sires were progeny tested and dams were sib tested. Sires and dams were selected by truncation on animal model BLUP EBVs. In SEsib, EBVs were based only on records of relatives in SE, whereas in CSPsib and CSPprog, EBVs were based on records of relatives in SE and PE. In addition to records of SE, in CSPsib sires and dams had records of half-sibs performing in PE, whereas in CSPprog sires had records of progeny performing in PE and dams had records of half-sibs (same animals as progeny of sires) performing in PE. A hierarchical mating structure was assumed and generations were discrete.

Table 1. Values of parameters used in calculating genetic gain in sib testing and progeny testing schemes: basic situation and range of values used in alternative breeding schemes.

Parameter	Basic	Alternatives	
		Range	Increment
Heritability (h^2)	0.3	0.05 to 0.6	0.05
Genetic correlation (r_g)	1.0	-1.0 to 1.0	0.1 / 0.01
Phenotypic variance (σ_p^2)	1.0		
Proportion selected sires (p)	0.05		
Number of progeny per dam (SE)[1]	8		
Number of animals in SE[1]	2000		200
Number of progeny tested sires (CSPprog)[2]	400		100
Number of PE[1] progeny / half-sibs per sire	100	10 to 500	10
Number of progeny per dam (PE)[1]	8		
Relative generation interval CSPprog sires[3]	1.4	1.0 to 2.0	0.1

1 SE = selection environment; PE = production environment.

2 SEsib = selection environment sib testing; CSPsib = combined selection environment and production environment sib testing; CSPprog = combined selection environment and production environment progeny testing; sires were progeny tested, while dams were sib tested like CSPsib.

3 Relative generation interval SEsib/CSPsib is 1.

Values of parameters are listed in Table 1. The generation interval of sires in CSPprog schemes was set relative to the generation interval of sires and dams in SEsib and CSPsib, so that one unit of time was equal to the generation interval of sires and dams in sib testing schemes (SEsib, CSPsib and dams in CSPprog). Based on species specific reproductive characteristics and time of measurement of trait, the relative generation interval of progeny tested sires was between 1.3 and 1.8 (e.g. Merks, 1988; Meuwissen, 1989). The basic situation represented a trait measured on both sexes before sexual maturity, e.g. growth rate. Reproductive characteristics represented the situation in pigs or poultry or in dairy cattle with multiple ovulation and embryo transfer (MOET). Alternative situations were created by changing one parameter at a time while keeping other parameters constant.

Genetic gain, relative genetic gain and break-even genetic correlation

Genetic gain per unit of time. Genetic gain was predicted deterministically by approximating BLUP-selection under an animal model using a pseudo-BLUP selection index (Wray and Hill, 1989; Villanueva et al., 1993). Genetic gain in the breeding goal (= PE) was predicted for sires and dams per generation. To take into account the longer generation interval of CSPprog, the formula of Rendel and Robertson (1950) was modified to two selection paths (sires and dams) to calculate genetic gain per unit of time, which was equal to the generation interval of sib testing schemes:

$$\Delta G = \frac{R_s + R_d}{L_s + L_d} = \frac{(i_s r_{IH,s} + i_d r_{IH,d})\sigma_H}{L_s + L_d} \qquad (1)$$

where

ΔG	= genetic gain per unit of time in the breeding goal,
R_s , R_d	= selection differential for sires and dams,
L_s , L_d	= generation interval relative to sib testing ($L_{sib} = 1$),
i_s , i_d	= selection intensity,
$r_{IH,s}$, $r_{IH,d}$	= accuracy of selection, and
σ_H^2	= genetic variance in the breeding goal.

Results were based on equilibrium genetic gain in the breeding goal per unit of time, accounting for build up of pedigree information (Dekkers, 1992) and reduction of genetic variance due to selection (Bulmer, 1971).

Selection intensity (i_s or i_d) was corrected for finite population size (Burrows, 1972) and correlated index values (Meuwissen, 1991). The approximation of Burrows (1972) was used to correct selection intensity for finite population size. Correlated index values of relatives in a finite population reduces the selection intensity because of a higher probability of selecting related selection candidates (Meuwissen, 1991). With increasing correlation between index values of relatives, selection moves from within families towards between families. The method of Meuwissen (1991), which is a 3-dimensional application of Rawlings (1976), was used to correct selection intensities for correlated index values of selection candidates. Correlations between index values of full-sibs and half-sibs were calculated as in De Boer and Van Arendonk (1991) and Bijma and Van Arendonk (1998).

Relative genetic gain. To measure loss in genetic gain due to G × E relative to no G × E ($r_g = 1$), relative genetic gain (ΔG_{rel}) was calculated as:

$$\Delta G_{rel} = \frac{\Delta G\ (r_g = x)}{\Delta G\ (r_g = 1)} = \frac{R_s(r_g = x) + R_d(r_g = x)}{R_s(r_g = 1) + R_d(r_g = 1)} \qquad (2)$$

Break-even genetic correlation. The rank order of breeding schemes based on genetic gain changes with decreasing genetic correlation. Rank changes of breeding schemes will occur at the "break-even" genetic correlation, i.e. when genetic gains of breeding schemes are equal. In this study, break-even genetic correlations were calculated to compare CSPprog with CSPsib and SEsib.

RESULTS

General

Figure 1 shows genetic gain per unit of time as a function of genetic correlation for SEsib, CSPsib and CSPprog. Genetic gain increased as genetic correlation approached unity or minus unity, at which genetic gain was similar for these breeding schemes. At unity genetic correlation genetic gain of CSPsib and SEsib were similar, because the extra information of half-sibs in PE in CSPsib did not add much to the accuracy of selection. Genetic gain of CSPprog was similar to genetic gain of SEsib and CSPsib, because of the choice of the relative generation interval of sires; for other values of the generation interval genetic gain per unit of time would have been different.

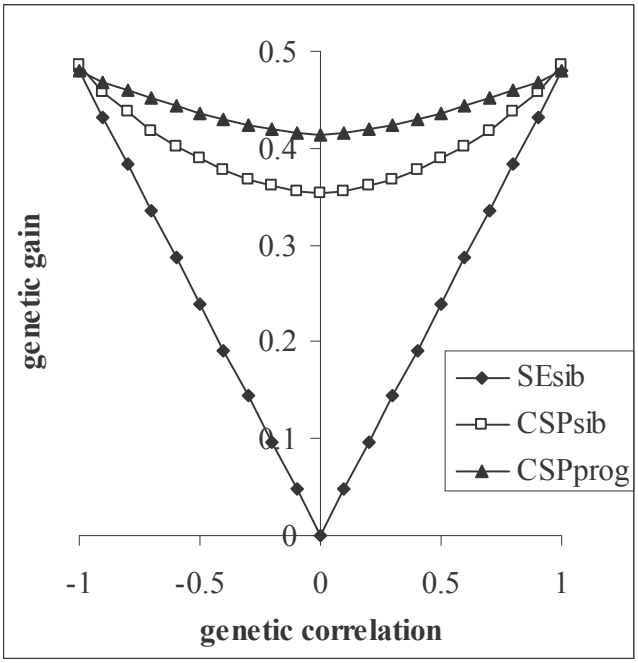

Figure 1. Genetic gain per unit of time as a function of genetic correlation for selection environment sib testing (SEsib), combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog) (heritability = 0.3; phenotypic variance = 1.0; proportion selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2000; number of progeny tested sires (CSPprog) = 400; number of production environment progeny per sire = 100; relative generation interval CSPprog sires = 1.4).

For these breeding schemes, genetic gain was different for correlations close to zero (Figure 1). Because differences were largest at zero genetic correlation, relative genetic gain will be presented at zero genetic correlation in Figures 2 and 3. In Figure 1, the effect of the genetic correlation on genetic gain was largest for SEsib and smallest for CSPprog. In SEsib, genetic gain in PE was purely a correlated response (straight lines) and relative genetic gain was equal to the genetic correlation (not shown). SEsib was therefore not included in Figure 2 and 3. The curves of CSPprog and CSPsib in Figure 1 showed that including information of relatives in PE in the index resulted in substantial genetic gain for every value of the genetic correlation and decreases, therefore, the loss in genetic gain due to G × E.

Heritability

Figure 2 shows relative genetic gain as a function of the heritability for CSPsib and CSPprog at genetic correlations of 0.5 and 0. Relative genetic gain was higher for CSPprog than for CSPsib, indicating a lower sensitivity for CSPprog to G × E. Relative genetic gain decreased as heritability increased. At high heritability and unity genetic correlation, own performance in SE is an important information source, but is of no importance at zero genetic correlation. With higher heritability the denominator of relative genetic gain (Equation 2) increased more than the numerator explaining the lower relative genetic gain. The decrease in relative genetic gain was smaller for CSPprog than for CSPsib for both values of the genetic correlation, because only the dam selection path contributed to loss in genetic gain.

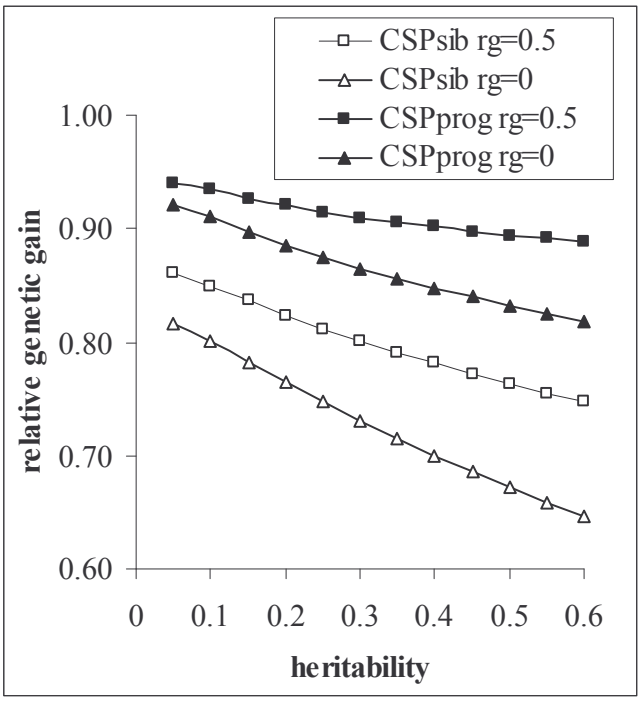

Figure 2. Relative genetic gain ($\Delta G(r_g = x) / \Delta G(r_g = 1)$; r_g = genetic correlation) as a function of heritability for combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog) at a genetic correlation (rg) of 0.5 and 0 (phenotypic variance = 1.0; proportion selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2000; number of progeny tested sires (CSPprog) = 400; number of production environment progeny per sire = 100; relative generation interval CSPprog sires = 1.4).

Number of PE progeny per sire

Figure 3 shows relative genetic gain at zero genetic correlation as a function of number of half-sibs per sire in PE for CSPsib and as a function of number of progeny per sire in PE for CSPprog. Relative genetic gain was higher for CSPprog than for CSPsib. Relative genetic gain increased asymptotically as number of progeny/half-sibs per sire increased. The asymptote was reached at a higher number of progeny/half-sibs for CSPsib than for CSPprog. More half-sibs/progeny per sire were necessary to reach the asymptote for a low heritability of 0.1 for CSPsib and CSPprog.

Generation interval

When generation interval of sires in CSPprog was varied, absolute genetic gain changed in opposite direction, but relative genetic gain was unaffected, because it is independent of the sum of the generation intervals (see Equation 2). However, when absolute genetic gain of CSPprog was compared to genetic gain of CSPsib or SEsib, generation interval of sires in CSPprog played an important role.

Figure 4 shows the break-even genetic correlation as a function of the generation interval of sires in CSPprog comparing CSPprog with SEsib or CSPsib. When the genetic correlation (0 – 1) was lower than the break-even genetic correlation, genetic gain of CSPprog was higher than genetic gain of SEsib or CSPsib, and vice versa. When the relative generation interval of CSPprog sires was short (e.g. 1.2), the break-even genetic correlation was 1, indicating that genetic gain of CSPprog was higher than genetic gain of CSPsib or SEsib. When the relative generation interval of CSPprog sires was more than 1.8, however, genetic gain of CSPprog was lower than genetic gain of CSPsib. When the relative generation interval of CSPprog sires was between 1.2 and 1.8 or 2.0, the break-even genetic correlation decreased as generation interval of sires of CSPprog increased relative to CSPsib and SEsib. The effect was larger comparing CSPprog with CSPsib than with SEsib. When heritability increased, the break-even genetic correlation decreased. Sib testing schemes, therefore, are relatively better than progeny testing schemes at higher heritability ($h^2 \geq 0.3$) and little G × E interaction

($r_g \geq 0.7$), whereas progeny testing schemes are better than sib testing schemes at lower heritability ($h^2 \leq 0.3$) or moderate to severe G × E interaction ($r_g \leq 0.8$).

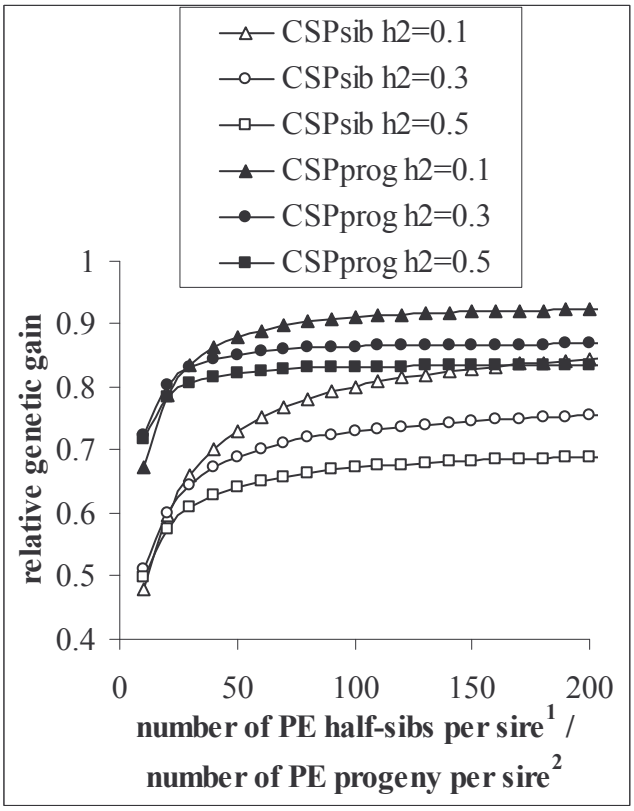

Figure 3. Relative genetic gain ($\Delta G(r_g = x) / \Delta G(r_g = 1)$; r_g = genetic correlation) as a function of number of half-sibs per sire[1] in production environment (PE) for combined selection environment and production environment sib testing (CSPsib) and relative genetic gain as a function of number of PE progeny per sire[2] for combined selection environment and production environment progeny testing (CSPprog) for zero genetic correlation and heritabilities (h2) of 0.1, 0.3 and 0.5 (phenotypic variance = 1.0; proportion selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2000; number of progeny tested sires (CSPprog) = 400; relative generation interval CSPprog sires = 1.4).

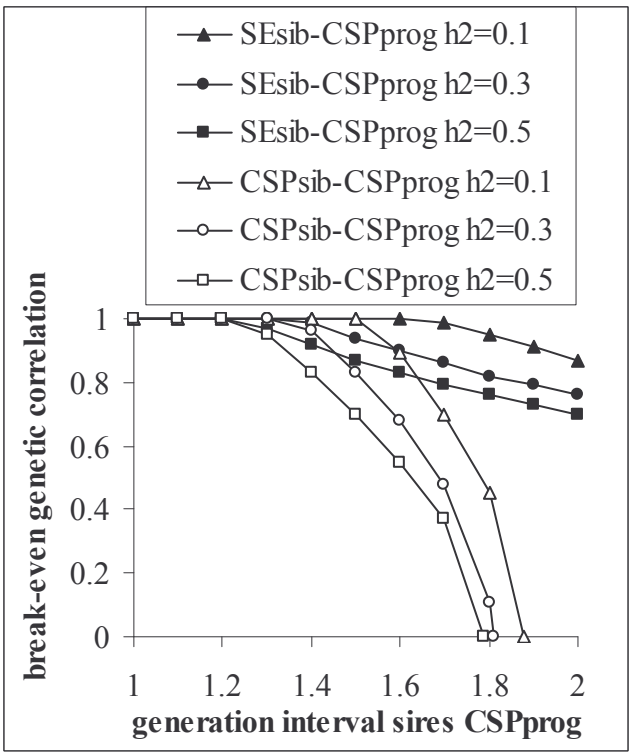

Figure 4. Break-even genetic correlation as a function of generation interval of sires in CSPprog comparing genetic gain of combined selection environment and production environment progeny testing (CSPprog) with genetic gain of combined selection environment and production environment sib testing (CSPsib) or selection environment sib testing (SEsib) for heritabilities (h2) of 0.1, 0.3 and 0.5 (phenotypic variance = 1.0; proportion selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2000; number of progeny tested sires (CSPprog) = 400; number of production environment progeny per sire = 100).

DISCUSSION

Results of selection environment sib testing (SEsib) versus combined selection environment and production environment sib testing (CSPsib) were in general similar to studies comparing pure line selection (PLS) with combined crossbred and purebred selection in pigs or poultry (CCPS) (Wei and Van der Werf, 1994; Bijma and Van Arendonk, 1998; Jiang and Groen, 1999). In these studies and in the present study, all selection candidates were located in a closed nucleus. The consequences of G × E for progeny testing schemes were studied by Meuwissen and Woolliams (1993) and Bondoc and Smith (1993), who simulated open nucleus situations in dairy cattle, where animals in the commercial population were selection candidates as well. The above studies are species specific, making it difficult to generalize and understand the effects of G × E on genetic gain in other breeding schemes. The uniqueness of this study is that effects of G × E on genetic gain were investigated in sib testing and progeny testing schemes using parameter values that represented pig, poultry and dairy cattle breeding schemes.

When G × E interaction plays a role in breeding schemes, different strategies can be used to deal with this interaction. Environmental strategies aim to reduce G × E by choosing a selection environment as similar as possible to commercial environments with respect to feeding regimen, housing system, or health status (Webb and Curran, 1986). In many situations, however, G × E can not be avoided, because it is beyond the control of breeders. In agreement with this study, Brascamp et al. (1985), Webb and Curran (1986) and Hartmann (1990) considered testing of half-sibs under commercial situations as a good option to maintain genetic gain in the presence of G × E in pig and poultry breeding schemes. Meuwissen and Woolliams (1993) concluded that dairy cattle open nucleus breeding schemes with progeny testing are robust for G × E.

Sib testing schemes had a higher loss in genetic gain due to G × E than progeny testing schemes. The concept of break-even genetic correlation, the value of the genetic correlation where genetic gain of different breeding schemes is equal, can be used to determine if sib testing or progeny testing is preferable. Costs of the breeding program and rate of inbreeding are other criteria to consider in deciding if sib testing or progeny testing is preferable. Progeny testing schemes are more expensive than sib testing schemes, because more progeny need to be produced and recorded and because housing costs of sires are higher due to the longer generation interval. Rates of inbreeding will favor progeny testing in the situation without G × E (Bovenhuis et al., 1989) and even more in the situation with increasing G × E, due to the increasing correlation between index values of relatives with sib testing, which causes a higher rate of inbreeding with sib testing (Burrows, 1984; Bijma et al., 2001). Economic aspects and rate of inbreeding must be considered when optimizing a specific breeding program.

CONCLUSION

Effects of G × E on genetic gain were investigated in sib testing and progeny testing schemes. Recording of half-sibs or progeny under commercial conditions limited the loss in genetic gain due to G × E between selection environment and production environment. Progeny testing schemes had a lower loss in genetic gain than sib testing schemes. Higher heritability resulted in a substantial higher loss in genetic gain, especially with sib testing, whereas increasing the number of progeny per sire in PE limited the loss. Progeny testing schemes were preferable in situations with low to moderate heritability ($h^2 \leq 0.3$), relative short generation interval of progeny tested sires ($L_{prog} / L_{sib} \leq 1.7$), and moderate to severe G × E interaction ($r_g \leq 0.8$). The concept of break-even genetic correlation (value of genetic

correlation where genetic gain is equal) is a helpful tool to determine if sib testing or progeny testing is preferable.

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