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Original Article

Variance components and animal rankings for milk yield and fat yield in a multibreed dairy cattle population using genomic-polygenic, genomic and polygenic models

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ABSTRACT

The variance ratios were estimated and animal rankings of genomic-polygenic (GP), genomic (G) and polygenic (P) models were compared for milk yield (MY) and fat yield (FY) in a Thai multibreed dairy cattle population. The dataset contained monthly records of MY and FY from 600 first-lactation cows from 56 farms in Central Thailand. The mixed model contained herd-year-season, Holstein fraction, heterozygosity of the cow and age at first calving as fixed effects (all models). Random effects were single nucleotide polymorphisms (SNP; GP and G models), animal polygenic (GP and P models) and the residual. The GP heritability estimates were higher for MY (0.38) and FY (0.41) than for the P model (0.28 for MY and 0.30 for FY). The fractions of the additive genetic variance explained by the SNP markers were 50% for MY and 48% for FY. Rank correlations between GP and G were the highest for both MY and FY (0.99; $p < 0.01$). Rank correlations between G and P were the lowest for MY (0.89; $p < 0.01$) and FY (0.73; $p < 0.01$). SNPs from the GeneSeek Genomic Profiler Low-Density (GGP-LD) 9k BeadChip not only accounted for a sizeable fraction of the additive genomic variance for MY and FY, but also yielded animal genomic estimated breeding values (EBV) whose rankings were highly correlated with the rankings of both genomic-polygenic and polygenic EBV. These results indicated that GGP-LD 9k and likely higher density genotyping chips would help improve the accuracy of prediction and selection in Central Thailand.

Introduction

Thailand is tropical and humid throughout the country during most of the year and the climate of Thailand is under the influence of seasonal monsoon weather (Thai Meteorological Department, 2014). This country is approximately 513,000 km^2 of which 46.53% is devoted to agriculture, 31.84% to non-agricultural endeavors and 21.63% to forests (Office of Agricultural Economics, 2014). Central Thailand has the largest concentration of dairy farms in an area comprising 26,900 km^2 and contains approximately 61% (145,578) of dairy cows on 62% (10,111) of dairy farms, which produce 64% (1,921,057 kg per day) of the milk produced in the country (Department of Livestock Development, 2015; Office of Agricultural Economics, 2015). Thai government policies in support of dairy farmer efforts to increase milk production have resulted in importation of Holstein semen and high-percent Holstein sires by the Dairy Farming Promotion Organization (DPO) and the Department of Livestock Development (DLD). The dairy cattle population in Central Thailand is multibreed, with its largest breed component being Holstein (H), accompanied by various fractions of other breeds (Brown Swiss, Jersey, Red Dane, Brahman, Red Sindhi, Sahiwal) and the parents in this population are chosen among purebred and crossbred Holstein animals resulting in a multibreed population composed of individuals with a variety of breed compositions (Koonawootrittriron et al., 2009). Currently, 90% of the population is over 75% H with small fractions of other breeds. This makes the structure of the Thai dairy population substantially different from dairy populations in other countries.

The main economically important traits in the Thai dairy business are milk yield (MY) and fat yield (FY) because they are associated directly with the amount of income received by dairy farmers. Milk composition such as FY has been used as an indicator

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of milk quality and considered for price determination of raw milk and dairy genetic improvement programs targeting such economically important traits have been used to select the best animals as parents of the next generation (Bourdon, 2000). The traditional genetic improvement for MY and FY in dairy cattle requires pedigree and phenotype information from individual animals. Traditional estimated breeding values (EBV) for animals are computed using best linear unbiased prediction (BLUP) procedures that utilize phenotype and pedigree information from all animals (Goddard and Hayes, 2007; Goddard et al., 2010; Vitezica et al., 2011).

Currently, single nucleotide polymorphisms (SNP) across the genome of individual animals can be determined from approximately 7000 SNPs up to more than 777,000 SNPs (Zhang et al., 2012). These SNPs provide an additional source of information to predict the genetic worth of an animal. The combination of genotyped SNPs, phenotype, and pedigree for animal evaluation has resulted in improved accuracies of prediction (Schaeffer, 2006; Hayes et al., 2009; Lillehammer et al., 2010). The current research assessed the advantage of utilizing SNP information for genetic prediction with and without pedigree information in multibreed dairy cattle from Central Thailand. Thus, the objectives of this study were: 1) to estimate the variance components, genetic parameters and fractions of genetic variances accounted by the GeneSeek Genomic Profile Low-Density (GGP-LD) BeadChip relative to total genetic variances; and 2) to compare animal rankings using predicted values from genomic-polygenic, genomic and polygenic models for milk yield and fat yield in a multibreed dairy cattle population in Central Thailand.

Materials and methods

Animal care

This research was approved by the Ethics Committee of the Kasetsart University Institutional Animal Care and Use Committee, Bangkok, Thailand and animal care and use under the Ethical Review Board of the Office of National Research Council of Thailand (ID: ACKU60-AGR-0090).

Data, traits and animal management

The dataset consisted of monthly test-day MY and FY from 600 first-lactation multibreed dairy cows that calved between 2000 and 2013 on 56 Central Thailand farms. These cows were the progeny of 198 sires and 547 dams. Cows, sires and dams in the Thai population were either purebred H or H crossbred with various amounts of genes from other breeds. Breeds represented in the Thai dairy population were Holstein, Brahman, Jersey, Red Dane, Red Sindhi, Sahiwal, and Thai Native. The H fraction of animals in this population ranged from 46.87% to 100%, and 91% of all animals were at least 75% H.

Cows were provided a concentrated diet for milk production at a rate of 1 kg of feed (16% protein) per 2 kg of milk. Roughage consisted mainly of fresh grasses such as Guinea grass (*Penicum maximum*), Ruzi grass (*Brachiaria ruziziensis*), Napier grass (*Pennisetum purpureum*) and Para grass (*Brachiaria mutica*). Fresh grass was limited during the dry season (November to June) due to dwindling supplies of stored and underground water. Farmers also fed rice straw and other agricultural by-products (corn cobs, cassava leaves, corn silage) when available. Cows were kept in open barns and milked twice a day; once in the morning (05:00–06:00 h) and once in the afternoon (14:00–15:00 h). Farmers used a bucket or a pipeline system for milking. Raw milk was collected in bulk tanks and transported to a dairy cooperative or to a private milk collection center after milking twice a day (morning and afternoon).

Traits were 305-d first lactation milk yield (MY, kilograms) and 305-d fat yield (FY, kilograms). Test-day MY and milk samples were taken from each individual cow once a month from calving to drying off. Milk samples were analyzed for fat percentage and other quality traits. Monthly test-day fat yields were computed as the product of fat percentage times test-day milk yield. Monthly test-day milk yields and fat yields were used to compute MY and FY using the test-interval method (Sargent et al., 1968; Koonawootrittriron et al., 2001). Contemporary groups were defined as herd-year-season of first calving. Calving age was defined as the number of months between birth date and calving date.

Blood sampling and single nucleotide polymorphisms

Blood samples were collected from the caudal vein (9 mL) and transported from farm to laboratory at the Faculty of Agriculture of Kasetsart University, Bangkok, Thailand. Genomic DNA was extracted from blood samples using a MasterPure™ DNA Purification Kit (Epicentre®; Madison, WI, USA). The concentration and purity of DNA per sample was measured using a NanoDrop 2000 (Thermo Fisher Science Inc.; Wilmington, DE, USA). DNA purity ratios of absorbance at 260 nm and 280 nm ranged from 1.8 to 2.0. The DNA concentration was in the range 9–645 ng/μL. DNA subsamples were dried using a freeze-dry machine in about 10–12 h. The dried DNA samples were prepared and transported by airmail from Kasetsart University to GeneSeek (GeneSeek; Lincoln, NE, USA) for genotyping using a GGP-LD. Only single nucleotide polymorphisms (SNP) from the 29 autosomes with call rates $\geq$ 90% and minor allele frequencies $\geq$ 0.01 were used in this research (n = 8257). The number of SNPs per chromosome ranged from 148 in chromosome 28 to 530 in chromosome 1 (Fig. 1).

Genomic-polygenic and polygenic variance components and variance ratios

Genomic-polygenic and polygenic variance components for MY and FY were estimated using the Markov Chain Monte Carlo (MCMC) procedure of GS3 with option VCE (Legarra et al., 2010). The genomic-polygenic model included the fixed effects of herd-year-season, the Holstein fraction of the cow, heterozygosity of the cow and age at first calving. Random effects were SNP, animal and the residual. The polygenic model included all the effects of the genomic-polygenic model, except for SNP random effects.

GS3 requires initial values for additive polygenic variance, residual variance, and additive SNP variances. Initial values for the additive polygenic variance and residual variance were estimated using an average information restricted maximum likelihood procedure with a model containing only additive polygenic effects using the ASREML software (Gilmour et al., 2006). Initial values for additive SNP variances were computed as the ASREML estimate of the additive polygenic variance divided by $\sum_{i=1}^{8257} 2p_iq_i$ (Habier et al., 2007; Gianola et al., 2009), where p_i = probability of allele A, and q_i = probability of allele B.

The genomic-polygenic variance component estimates from GS3 were the additive SNP variances (VSNP), additive polygenic variances (VAPO) and residual variance (VE). Genomic-polygenic variance components (additive genomic variances, VAGO; additive polygenic variances, VAPO; additive total genetic variances, VGTot; phenotypic variances, PheVarGP) were computed using GS3 (option VCE). Additive genomic variances were computed as the product of $\sum_{i=1}^{8257} 2p_iq_i$ times VSNP. Total genetic variances were computed as VAGO + VAPO. Phenotypic variances were computed as VAGO + VAPO + VE.

Polygenic variance component estimates were the additive polygenic variances (VGPO) and residual variances (VE). Polygenic variance components were also computed using option VCE of the MCMC procedure of the GS3 program. Phenotypic variances were

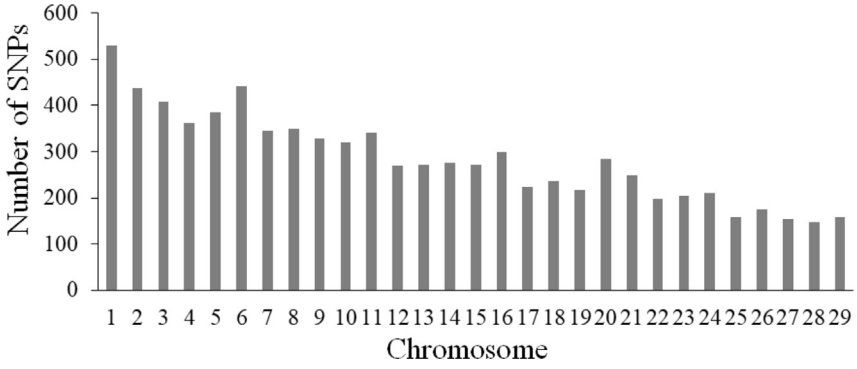

Fig. 1. Number of single nucleotide polymorphisms (SNPs) in each bovine chromosome.

computed as VAPO + VE. The variance ratios and heritabilities for MY and FY were computed using the estimated variances.

The estimates and variability of the genomic-polygenic, genomic and polygenic variance components and genetic parameters in the population were obtained as the mean and SD, respectively, of their sample values across all MCMC samples (number of MCMC samples = 1200).

Genomic-polygenic, genomic and polygenic predictions

The genomic-polygenic, genomic and polygenic predictions for MY and FY used VAGO, VAPO and VE values computed using the GS3 option BLUP (Legarra et al., 2010). The genomic-polygenic predictions were obtained using a genomic-polygenic model. The genomic predictions were obtained using a genomic model (a genomic-polygenic model without an animal random effect). The polygenic predictions were obtained using a polygenic model (a genomic-polygenic model without an SNP random effect).

Genomic-polygenic EBV (GPEBV) values were computed using Equation (1):

$$\text{GPEBV} = (\beta_{HF})(\text{HF}) + \text{additive genomic value} + \text{additive polygenic value} \quad (1)$$

where β_{HF} are the regression coefficient estimates for the Holstein fraction, HF is the Holstein fraction of cows, the additive genomic value is $\sum_{i=1}^{8257} w_i \widehat{SNP}_i$, where w_i is the number of B alleles in locus i, $\widehat{SNP}_i$ is the BLUP of SNP_i, and the additive polygenic value is the BLUP of the animal random effect from the genomic-polygenic model.

Genomic EBV (GEBV) was computed using Equation (2):

$$\text{GEBV} = (\beta_{HF})(\text{HF}) + \text{additive genomic value} \quad (2)$$

where β_{HF} are the regression coefficient estimates for the Holstein fraction, HF is the Holstein fraction of cows and the additive genomic value is $\sum_{i=1}^{8257} w_i \widehat{SNP}_i$, where w_i is the number of B alleles in locus I and $\widehat{SNP}_i$ is the BLUP of SNP_i from the genomic model.

Polygenic EBV (PEBV) was computed using Equation (3):

$$\text{PEBV} = (\beta_{HF})(\text{HF}) + \text{additive polygenic value} \quad (3)$$

where β_{HF} are the regression coefficient estimates for the Holstein fraction, HF is the Holstein fraction of cows and the additive polygenic value is the BLUP of the animal random effect from the polygenic model.

Animal rankings of BLUP predictions from genomic-polygenic, genomic and polygenic models were analyzed using Spearman's rank correlations (SAS, 2003).

Results and discussion

Genomic-polygenic and polygenic variance components for MY and FY are presented in Table 1. The additive genomic variances from the GP model were 215.44 (SD = 127.96) kg^2 for FY and 122,763 (SD = 70,598) kg^2 for MY. The additive polygenic variances from the GP model were 252.86 (SD = 192.14) kg^2 for FY and 129,064 (SD = 87,924) kg^2 for MY. The total genetic variances from the GP model were 468.31 (SD = 203.84) kg^2 for FY and 251,828 (SD = 97,589) kg^2 for MY. The phenotypic variances from the GP model were 1131.92 (SD = 111.83) kg^2 for FY and 659,615 (SD = 51,580) kg^2 for MY. The additive genetic variances from the P model were 335.17 (SD = 210.10) kg^2 for FY and 183,452 (SD = 100,431) kg^2 for MY. The phenotypic variances from the P model were 1097.02 (SD = 108.82) kg^2 for FY and 645,573 (SD = 50,627) kg^2 for MY.

Variance ratios and heritability from GP and P are shown in Table 2. The GP heritability estimates were 0.38 for MY and 0.41 for FY. The P heritability estimates were 0.28 for MY and 0.30 for FY. These P heritabilities were within the range 0.29–0.41 for MY, and 0.29–0.39 for FY in Dutch and Nordic Holstein Friesian populations (Stoop et al., 2008; Schopen et al., 2009; Gao et al., 2012). The P heritabilities for MY and FY were lower than in the UK Holstein Friesian population (Pollott, 2009; Eaglen et al., 2013). The GP heritability estimates were lower than the range 0.41–0.80 for MY, and 0.42–0.77 for FY in Dutch and Australian Holstein Friesian populations (Veerkamp et al., 2010, 2011; Haile-Mariam et al., 2013). The GP variances and heritabilities were higher than those of the P model. The GP heritabilities for MY and FY were slightly higher than the estimates from P models in Australia

Table 1
Posterior means (SD in parentheses) of variance components for milk yield (MY) and fat yield (FY) from genomic-polygenic and polygenic models.

Variance component	Traits	
	MY (kg^2)	FY (kg^2)
VAGO	122,763 (70,598)	215.44 (127.96)
VAPO	129,064 (87,924)	252.86 (192.14)
VGTot	251,828 (97,589)	468.31 (203.84)
PheVarGP	659,615 (51,580)	1131.92 (111.83)
VGPO	183,452 (100,431)	335.17 (210.10)
PheVarP	645,573 (50,627)	1097.02 (108.82)

VAGO = additive genomic variances, VAPO = additive polygenic variances, VGTot = total genetic variances, PheVarGP = phenotypic variances from the genomic-polygenic model, VGPO = additive genetic variances from the polygenic model, PheVarP = phenotypic variances from the polygenic model.

Table 2
Posterior means (SD in parentheses) of variance ratios and heritability for milk yield (MY) and fat yield (FY).

Variance ratio	Traits	
	MY	FY
VAGO/VGTot	0.50 (0.23)	0.48 (0.24)
HeritabilityGP	0.38 (0.13)	0.41 (0.16)
HeritabilityP	0.28 (0.14)	0.30 (0.18)

VAGO = additive genomic variances, VGTot = total genetic variances, HeritabilityGP = heritability from genomic-polygenic model, HeritabilityP = heritability from polygenic model.

(Haile-Mariam et al., 2013), but slightly lower than in the Netherlands (Veerkamp et al., 2010). Differences between variances and heritability estimates in the Thai population versus those from other countries may have been related to the number of SNPs in the analyses, linkage disequilibrium between SNPs and genes affecting MY and FY in each population, the size of reference populations, the statistical models used in each country and the population structure across countries. The Thai population is multibreed with a larger representation of H than from six other breeds (Brahman, Jersey, Red Dane, Red Sindhi, Sahiwal, Thai Native). In fact, over 80% of the animals in the Thai population have a Holstein fraction higher than 75% (Koonawootrittriron et al., 2009; Ritsawai et al., 2014; Jattawa et al., 2015).

The ratios of the additive genomic variances to the total genetic variances from the GP model were high for MY (50%) and FY (48%; Table 2). These percentages indicated that the genomic information of the GGP-LD 9k BeadChip captured a substantial percentage of the total genetic variation for MY and FY in this multibreed dairy cattle population in Central Thailand. The estimates of variances and heritabilities in this study indicated that it would be feasible to increase MY and FY using genetic selection under Thai tropical conditions. Further gains could be achieved by improving management practices and feeding regimes (such as good quality forage throughout the year) to meet the needs of cows with high genetic production ability. Milk production in Central Thailand has been substantially increased through crossbreeding programs aimed at improving native and crossbred varieties to Holstein and both purebred and crossbred Holstein cattle have been selected as

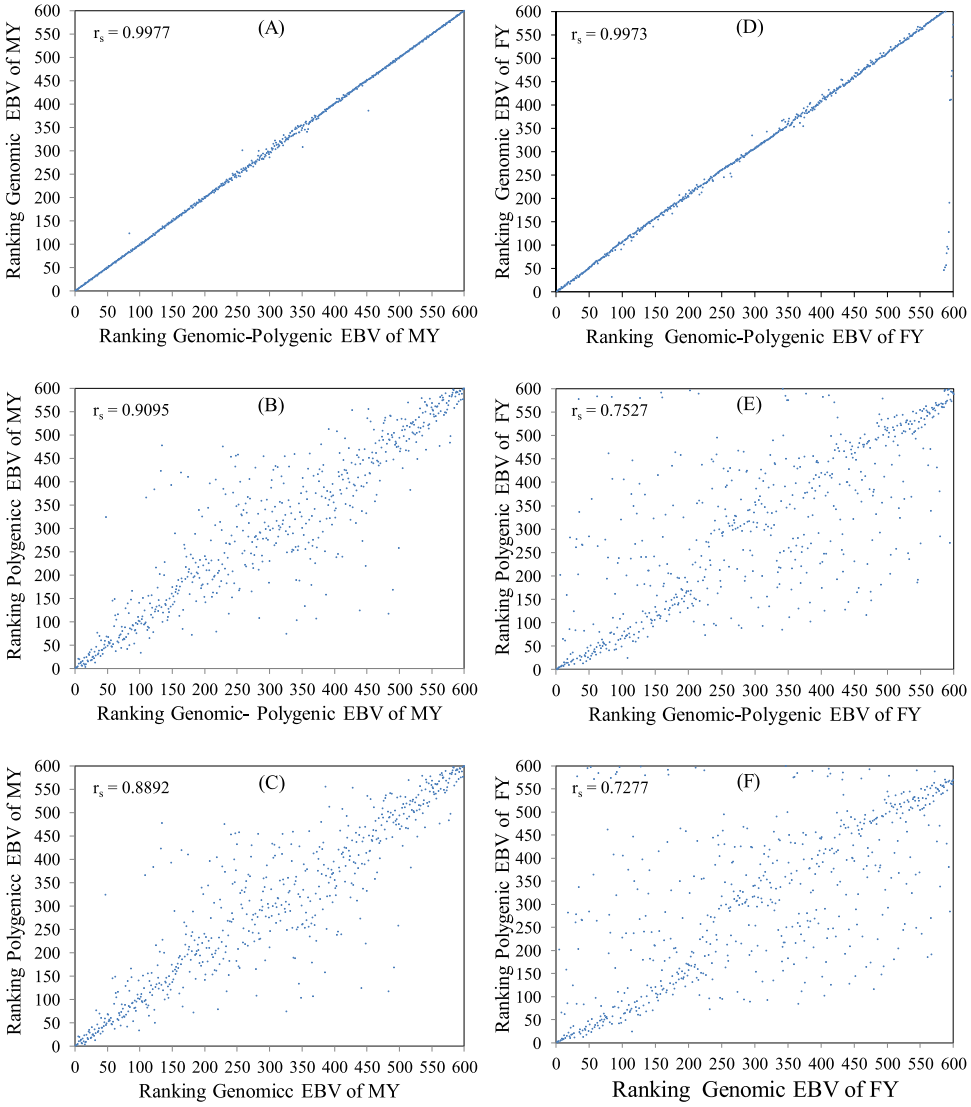

Fig. 2. Spearman's rank correlation (r_s): (A) between genomic-polygenic (GP), genomic (G) estimated breeding value (EBV) model of milk yield (MY); (B) between GP and polygenic (P) EBV model of MY; (C) G and P estimated breeding value model of MY; (D) GP and G EBV model of fat yield (FY); (E) GP and P EBV model of FY; (F) G and G EBV model of FY, where all Spearman's rank correlations were significant ($P < 0.0001$).

parents of future generations (Koonawootrittriron et al., 2009). This practice of identifying the best males and females regardless of breed composition should continue to help increase MY and FY in future years.

Spearman's rank correlations among the genomic-polygenic, genomic and polygenic predictions for MY and FY are shown in Fig. 2. Rank correlations between GP and G were 0.9973 for FY and 0.9977 for MY ($p < 0.0001$). Rank correlations between GP and P were 0.7527 for FY and 0.9095 for MY ($p < 0.0001$). Rank correlations between G and P were 0.7277 for FY and 0.8892 for MY ($p < 0.0001$). The correlations among GP, G and P were high for MY and FY. For MY, the rank correlation between GP and G (0.9977; $p < 0.0001$) was stronger than the correlations between GP and P (0.9095; $p < 0.0001$) and between G and P (0.8892; $p < 0.0001$). For FY, the correlation between GP and G (0.9973; $p < 0.0001$) was stronger than the correlations between GP and P (0.7527; $p < 0.0001$) and between G and P (0.7277; $p < 0.0001$). These high correlations indicated the possibility of preselecting young animals for MY and FY using the G model to reduce the generation interval and decrease evaluation costs. After cow phenotypes are collected, final genetic evaluations can be performed using the GP model.

In conclusion, the fractions of additive genomic variances from the GP model were high, 50% for MY and 48% for FY. The heritability estimates with the GP model were higher for MY (0.38) and for FY (0.41) than for the P model MY (0.28) and for FY (0.30). The rank correlations between GP and G were stronger than those between GP and P and between G and P. This research indicated that genomic information from the bovine chip with 8257 SNPs could be used in addition to phenotypic and pedigree information to improve prediction accuracies in this multibreed dairy cattle population in Central Thailand.

Conflict of interest

The authors declare that they have no conflict of interest.

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