

# Genetic interrelationships among phosphorus, nitrogen, calcium, and energy bioavailability in a growing chicken population

G. A. Ankra-Badu, G. M. Pesti, and S. E. Aggrey<sup>1</sup>

*Department of Poultry Science, University of Georgia, Athens 30602*

**ABSTRACT** A random-mating population was used to study the genetic interrelationship between phytate P (PPB), Ca (CaB), N (NB), and energy bioavailability (EB), BW at 4 wk of age, relative growth (RG), and feed conversion ratio (FCR). Heritability estimates for PPB, CaB, NB, and EB were 0.09, 0.13, 0.16, and 0.10, respectively, and those of BW, RG, and FCR were 0.66, 0.15, and 0.10, respectively. Genetic correlations between PPB and BW, and FCR were moderate and negative, suggesting that improvement in PPB will impair growth. The genetic correlations between PPB and CaB, and EB and RG were positive and moderate, indicating that improvement in PPB would also lead to improved CaB, EB, and RG. Energy bioavailability was positively correlated with CaB, NB, PPB, and BW.

Even though the genetic correlation between EB and the other traits measured, except RG and FCR, ranged from low to moderate, improving the ability of birds to utilize caloric energy in the feed would consequently improve PPB as well as growth. Improving PPB would reduce the amount of P in excreta and provide an additional savings if exogenous phytase were not added to poultry feed. The genetic correlation between PPB and NB was low but positive, whereas NB had a positive genetic correlation with BW. Therefore, selecting on NB will result in positive correlated responses in BW and PPB. Improving PPB and NB will not only improve productivity, but also reduce the polluting effects of P and N on the environment.

**Key words:** sustainability, phosphorus bioavailability, nitrogen bioavailability, calcium bioavailability, energy bioavailability

2010 Poultry Science 89:2351–2355  
doi:10.3382/ps.2010-00870

## INTRODUCTION

Phosphorus is an important mineral required in poultry diets for normal growth and development. It plays an important role in the metabolism of carbohydrates, amino acids, lipids, and energy. Poultry diets are made primarily of ingredients of plant origin, including cereal grains, cereal by-products, and oilseed meals. The main sources of P in plant tissues are phosphates, phytate, and other myo-inositol phosphates (Classen and Stevens, 1995; Sebastian et al., 1996). Phytates are largely unavailable to monogastrics because they lack significant sources of intestinal phytase (Nelson, 1967; Kornegay, 1996). Phytase makes P available by removing phosphate groups from the inositol hexaphosphate (phytate) molecule (Sandberg et al., 1993) by releasing P for absorption and utilization. The inability of monogastrics to utilize phytate P results in a substantial loss of nutrient efficiency and creates an

important pollution threat when manure containing residual P is applied to land. The addition of microbial phytase to the diet has been found to improve phytase P bioavailability (**PPB**) (Kornegay, 1996). The efficacy of microbial phytase, however, is influenced by several factors, including vitamin D (Mohammed et al., 1991; Edwards, 1993), Ca-to-total P ratio (Liu et al., 1998), Ca bioavailability (**CaB**), the presence of inorganic P (**iP**) supplements, age (Kornegay, 1996), size of the bird (Punna and Roland, 1999), and level of phytase in the diet (Shirley and Edwards, 2003).

Several studies have shown variability in PPB, ranging from zero (Nelson, 1967) to more than 50% (Edwards, 1983), depending on the strain (Edwards, 1983), age, ingredient type, dietary levels of Ca and iP (Ravindran et al., 1995), and vitamin D (Edwards, 1993). The genetic basis for PPB was first established by Zhang et al. (2003). Because PPB is affected by Ca, vitamin D, and the size of the bird, variability in any of these factors would invariably affect PPB. The objective of this study was to ascertain the genetic interrelationships among growth, PPB, CaB, N bioavailability (**NB**), and energy bioavailability (**EB**) in a growing chicken population. Genetic interrelationships are required for devis-

©2010 Poultry Science Association Inc.

Received May 3, 2010.

Accepted August 15, 2010.

<sup>1</sup>Corresponding author: saggrey@uga.edu

ing breeding strategies to improve NB and P bioavailability while maintaining or improving growth.

## MATERIALS AND METHODS

### Birds

A pedigreed population was established from mating 40 male and 200 female chickens (sex ratio ~1:2 or 1:3) of the Athens Canadian randombred population (Hess, 1962) to hatch 1,004 chicks in 6 hatches at 7-d intervals. Chicks were placed in pens with litter and fed a corn- and soybean meal-based diet containing 23% protein, 3,200 kcal of ME/kg, 0.90% Ca, 0.675% total P, and 0.45% available P until 4 wk of age. Shortly thereafter, the birds were transferred to individual cages and fed the same diet with iP largely removed and Ca and total P adjusted to 1.06 and 0.35%, respectively. After 3 d of acclimation, feed consumption was measured and the excreta produced in 3 consecutive days were collected. Individual BW at the beginning and end of the 3-d excreta collection period were also measured. Excreta were oven-dried at 80°C and ground. Phytate P in the feed and dried excreta was determined by the method described by Latta and Eskim (1980). Nitrogen and Ca in 100 fecal samples and a representative sample of the feed were determined by the methods described by AOAC (1995) and Hill (1965), respectively. Energy in feed and excreta in the 100 samples were determined by bomb calorimetry (Parr Instrument Co., Moline, IL). The 100 fecal samples and a representative sample of the feed were scanned in a near-infrared spectrophotometer (NIRS) with NIRS-2 Software (Feed and Forage Analyzer Model 5000, Foss NIRSystems Inc., Eden Prairie, MN). The samples were used to create calibration curves for the NIRS. Based on these calibrations, N, Ca, and energy content of the 1,004 excreta samples were estimated by the NIRS method. The efficiencies of NIRS in predicting Ca, N, and energy have been described (Smith et al., 2001). Feed conversion ratio (FCR) was calculated as the ratio of feed consumption to BW gain. The bioavailability of phytate P, Ca, N, and energy was also computed as follows:

$$\text{NBA} = (A - B)/(A \times 100\%),$$

where NBA is nutrient bioavailability, A is nutrient content of the feed (%)  $\times$  feed intake (g), and B is nutrient content of dried excreta (%)  $\times$  dried excreta weight (g). Relative growth (RG), PPB, CaB, NB, and EB data were collected on 1,004 birds. Energy bioavailability is equivalent to AME; however, for consistency, EB is used in this paper.

### Data Editing and Statistical Analysis

Data editing was done by obtaining descriptive statistics by using the PROC MEANS and PROC UNI-

VARIATE methods (SAS Institute, 1998). Individual records that were more than 3 SD from the mean were classified as outliers and removed. After data editing, 919 individuals (476 males and 443 females) with complete records of all the traits measured from 26 sires and 71 dams, and 105 (44 males and 61 females) grandparents were used for estimation of genetic parameters. Mixed animal models (Mrode, 1996) and restricted maximum likelihood methods (Henderson, 1985) were used for estimating the variance components of the traits measured. The animal model used was

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

where  $\mathbf{y} = (\mathbf{y}'_1 \mathbf{y}'_2 \dots \mathbf{y}'_t)'$ , and  $\mathbf{y}'_t$  is a vector of phenotypic observations for trait  $t$ ;  $\mathbf{X}$  is a matrix that relates fixed effects to the phenotypic record;  $\mathbf{Z}$  is a matrix that relates animals to the records;  $\boldsymbol{\beta} = (\boldsymbol{\beta}'_1, \boldsymbol{\beta}'_2, \dots, \boldsymbol{\beta}'_t)'$ , and  $\boldsymbol{\beta}'_t$  is a vector of fixed effects for trait  $t$ ;  $\mathbf{u} = (\mathbf{u}'_1, \mathbf{u}'_2, \dots, \mathbf{u}'_t)'$ , and  $\mathbf{u}'_t$  is a vector of random animal effects for trait  $t$ ; and  $\mathbf{e} = (\mathbf{e}'_1, \mathbf{e}'_2, \dots, \mathbf{e}'_t)'$ , and  $\mathbf{e}'_t$  is a vector of residual effects for trait  $t$ . The variances of random animal effects were  $\text{var}(\mathbf{u}) = \mathbf{A} \otimes \mathbf{G}$  and  $\text{var}(\mathbf{e}) = \mathbf{I} \otimes \mathbf{R}$ , where  $\mathbf{A}$  is the additive relationship matrix,  $\mathbf{G}$  is the (co)variance matrix for genetic effects of the traits,  $\mathbf{I}$  is the identity matrix, and  $\mathbf{R}$  is the (co)variance matrix for the corresponding residual effects. Sex and hatch groups were considered fixed effects. Heritability estimates, and genetic and phenotypic correlations were estimated for BW, FCR, RG, PPB, CaB, NB, and EB. A bivariate model was used to estimate the genetic and phenotypic correlations. Pedigree information of the parents was used and the formation of the inverse of the  $\mathbf{A}$  matrix ( $\mathbf{A}^{-1}$ ) was based on the methods of Henderson (1975) and Quaas (1976). The estimations of variance components were accomplished with the average information algorithm for restricted maximum likelihood (Johnson and Thompson, 1995). Convergence was considered to have been reached when

$$(\hat{\boldsymbol{\theta}}_t - \hat{\boldsymbol{\theta}}_{t-1})'(\hat{\boldsymbol{\theta}}_t - \hat{\boldsymbol{\theta}}) / \hat{\boldsymbol{\theta}}_t' \hat{\boldsymbol{\theta}}_t < 5 \times 10^{-11},$$

where  $\hat{\boldsymbol{\theta}}_t$  is a vector of estimated parameters in the  $t$ th iteration. The estimates of genetic parameters were calculated according to the definitions of Falconer and Mackay (1996) and were obtained from the estimated (co)variance matrices for genetic and residual effects. The SE of heritability were based on the asymptotic variances of  $f(\hat{\boldsymbol{\theta}}_t)$  (Stuard and Ord, 1994; Dodenhoff et al., 1998) and were calculated as

$$SE(h^2) \approx \sqrt{\left\{ \frac{\partial h^2}{\partial \theta'} \right\} \text{var}(\hat{\theta}) \left\{ \frac{\partial h^2}{\partial \theta} \right\}} \frac{\partial h^2}{\partial \theta'} = \left[ \frac{h^2 - h^4}{\sigma_a^2} - \frac{h^4}{\sigma_e^2} \right],$$

where  $\text{var}(\hat{\theta})$  is composed of the elements of an asymptotic dispersion matrix of the estimated parameters [(co)variance components], which is the inverse of the negative average information matrix. For  $SE(h^2)$ ,  $\theta = [\sigma_a^2, \sigma_e^2]'$ .

## RESULTS AND DISCUSSION

Analysis of variance (data not shown) showed that there were differences ( $P \leq 0.05$ ) among hatch groups for all traits. The data were corrected for hatch group and sex effects, and least squares means, SD, minimum and maximum values, and heritability estimates for the traits measured are listed in Table 1. The heritability estimates of BW and FCR were 0.66 and 0.10, respectively. The estimate for BW is consistent with values reported in the literature (Chambers, 1990), but the estimate for FCR was lower than the 0.2 to 0.4 reported by Chambers et al. (1994). As suggested by McCarthy and Siegel (1983) and Marks (1991), the maintenance requirement may substantially mask genetic variation in feed efficiency for growth at a young age. The heritability of RG was 0.15. Whereas BW at a specified age measures absolute growth, RG assesses the efficiency of a bird to synthesize new mass (Aggrey, 2003).

The heritability estimates of PPB, CaB, NB, and EB were 0.09, 0.13, 0.16, and 0.10, respectively. Zhang et al. (2003) reported on the heritability of PPB, but estimates for CaB, NB, and EB have not been published in the poultry literature. The SE associated with the heritability estimates were low, indicating that additive genetic variances are associated with the bioavailability traits measured in this population. However, a direct response to mass selection of any of the bioavailability traits is expected to be slow. Zhang et al. (2003) reported on a negative genetic correlation between PPB and growth. Short-term divergent selection for PPB demonstrated a moderate response (Zhang et al., 2005a) and a negative correlated response in growth, as predicted

from the genetic correlation of the base population (Zhang et al., 2005b).

Phenotypic and genetic correlations among traits are reported in Table 2. The phenotypic correlation between BW and FCR was consistent with literature reports (Chambers, 1990; Chambers et al., 1994). The genetic correlations between PPB and CaB, and EB and RG were positive and moderate, suggesting that improvement in PPB would also lead to increased bioavailability of Ca and energy, as well as efficiency of growth. The positive genetic correlation between PPB and CaB was expected because there is an interaction between the metabolism of Ca and P. The homeostatic metabolism of both minerals is controlled by similar mechanisms (Georgievski, 1982). An improvement in skeletal Ca retention is accompanied by improved retention of P because Ca is only well utilized for skeletal growth when P is available at the same time (Helander et al., 1996; Underwood and Suttle, 1999). The active form of vitamin D, 1,25-dihydroxycholecalciferol, stimulates Ca uptake and improves its absorption. An increase in Ca absorption also leads to an increase in the level of P and favors the deposition of these minerals in the bone (Edwards, 1993). Edwards and Veltmann (1983) showed that P retention depends on the levels of both Ca and P in the diet, and their retentions are highest when the levels of these elements are low. The genetic correlation between CaB and BW was negative and low, indicating that selection for CaB would impair growth.

Energy bioavailability was positively correlated with CaB, NB, PPB, and BW. Even though the genetic correlation between EB and the other traits measured (except RG and FCR) ranged from low to moderate for the Athens Canadian randombred population, improving the ability of birds to utilize caloric energy from the feed would consequently improve PPB as well as growth. Phosphorus plays an important role in the utilization and transfer of energy (Underwood and Suttle, 1999). Phosphorus is vital for the formation of adenosine triphosphate and adenosine diphosphate, which are required for the release of energy. The inability of a bird to generate P for energy use would be detrimental to its growth and normal development. Therefore, it should not be surprising to observe a positive genetic correlation between EB and PPB. Energy bioavailabil-

**Table 1.** Least squares means and estimates of heritability for BW, relative growth (RG), feed conversion ratio (FCR), phytate P bioavailability (PPB), Ca bioavailability (CaB), N bioavailability (NB), and energy bioavailability (EB)

Trait	Least squares mean $\pm$ SD	Minimum	Maximum	$h^2 \pm$ SE
BW, 4 wk/g	291.52 $\pm$ 41.87	129.54	425.73	0.66 $\pm$ 0.07
RG, g/g per day	0.15 $\pm$ 0.04	0.06	0.34	0.15 $\pm$ 0.01
FCR, g/g	2.38 $\pm$ 0.41	1.06	4.15	0.10 $\pm$ 0.03
PPB, %	32.02 $\pm$ 6.79	5.05	61.11	0.09 $\pm$ 0.03
CaB, %	24.41 $\pm$ 9.76	2.41	77.16	0.13 $\pm$ 0.01
NB, %	59.36 $\pm$ 4.27	38.21	78.21	0.16 $\pm$ 0.01
EB, %	82.55 $\pm$ 1.49	77.47	89.18	0.10 $\pm$ 0.04

**Table 2.** Genetic correlations (above diagonal) and phenotypic correlations of BW, relative growth (RG), feed conversion ratio (FCR), phytate P bioavailability (PPB), Ca bioavailability (CaB), N bioavailability (NB), and energy bioavailability (EB)

Item	BW	RG	FCR	PPB	CaB	NB	EB
BW		-0.39	-0.10	-0.25	-0.13	0.50	0.37
RG	-0.25		-0.71	0.55	0.37	-0.23	-0.23
FCR	0.11	-0.73		-0.55	-0.58	0.03	-0.25
PPB	-0.12	0.17	-0.20		0.55	0.19	0.51
CaB	-0.10	0.21	-0.26	0.63		-0.37	0.29
NB	0.06	0.08	-0.12	0.65	0.33		0.61
EB	-0.01	0.11	-0.18	0.79	0.53	0.80	

ity is easy to measure with a high degree of accuracy compared with CaB, NB, and PPB. Incorporating EB into a selection index for genetic improvement would consequently improve growth, PPB, CaB, and NB. The genetic correlation between PPB and NB was low but positive, whereas NB had a positive genetic correlation with BW. Therefore, selecting on NB will result in positive correlated responses in BW and PPB, and a decline in CaB. A decline in CaB has the potential to affect skeletal integrity.

Protein and amino acids in feed that are not digested and absorbed are excreted as N. Nitrogen can be converted into nitrates, which is a water quality concern because nitrates have been linked to methemoglobinemia in infants, toxicity in livestock, and eutrophication in both fresh and saline waters (Sharpley et al., 1998). Phosphorus in water is not considered to be directly toxic to humans and animals and, as a result, no drinking water standards have been established for P (US Environmental Protection Agency, 1990). However, eutrophication of surface water restricts its use for fisheries, recreation, industry, and drinking because of the increased growth of undesirable algae and aquatic weeds and oxygen shortages caused by their senescence and decomposition. Therefore, improving PPB and NB will not only improve productivity, but will also reduce the polluting effects of P and N on the environment.

The current study is the first report on the genetic interrelationships between growth and feed nutrient bioavailability. A breeding strategy can be devised to improve the absorption and utilization of nutrients. Most important, improving the bioavailability of phytate P would reduce the amount of P in excreta and provide an additional savings from exogenous phytase added to poultry feed. However, it would be worthwhile to examine the same interrelationships in commercial lines and collect data for a longer time.

## ACKNOWLEDGMENTS

The authors thank Ignacy Misztal (Department of Poultry Science, University of Georgia, Athens) for use of his program, and Cheryl Pearson Gresham (Department of Poultry Science, University of Georgia, Athens) for her technical assistance. This research was supported by funds from the US Poultry and Egg Association (Tucker, GA) and State and Hatch funds allocated to

the Georgia Agricultural Experimental Stations of the University of Georgia.

## REFERENCES

- Aggrey, S. E. 2003. Dynamics of relative growth in Japanese quail lines divergently selected for growth and their control. *Growth Dev. Aging* 67:47-54.
- AOAC. 1995. *Official Methods of Analysis*. 16th ed. Assoc. Off. Anal. Chem., Washington, DC.
- Chambers, J. R. 1990. Quantitative genetics and selection. Pages 599-643 in *Poultry Breeding and Genetics*. R. D. Crawford, ed. Elsevier, Amsterdam, the Netherlands.
- Chambers, J. R., I. Wang, and I. McMillan. 1994. Genetic variation of broiler feed consumption and efficiency corrected for differences in test body weights. *Poult. Sci.* 73:1196-1203.
- Classen, H. L., and J. P. Stevens. 1995. *Nutrition and growth*. Pages 79-99 in *Poultry Production*, World Animal Science. P. Hunton, ed. Elsevier, Amsterdam, the Netherlands.
- Dodenhoff, J., L. D. van Vleck, S. D. Kachman, and R. M. Kock. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* 76:2521-2527.
- Edwards, H. M. Jr 1983. Phosphorous I. Effect of breed and strain on utilization of sub-optimal level of phosphorous in ration. *Poult. Sci.* 62:77-84.
- Edwards, H. M. Jr 1993. Dietary 1,25-dihydroxycholecalciferol supplementation increases natural phytate phosphorus utilization in chickens. *J. Nutr.* 123:567-577.
- Edwards, H. M. Jr., and J. R. Veltmann. 1983. The role of calcium and phosphorus in the etiology of tibial dyschondroplasia in young chicks. *J. Nutr.* 113:1568-1575.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. Longman Group Ltd., Essex, UK.
- Georgievski, V. I. 1982. General information on minerals. Pages 11-55 in *Mineral Nutrition of Animals*. V. I. Georgievski, B. V. Annenkov, and V. I. Samokhin, ed. Butterworths, London, UK.
- Helander, E., M. Nasi, and K. Partanen. 1996. Effects of supplementary *Aspergillus niger* phytase on the availability of plant phosphorus, other minerals and nutrients in growing pigs fed on high pea diets. *J. Anim. Physiol. Nutr.* 76:66-79.
- Henderson, C. R. 1975. Rapid method for computing the inverse of a relationship matrix. *J. Dairy Sci.* 58:1727-1730.
- Henderson, C. R. 1985. MIVQUE and REML estimation of additive and non-additive genetic variances. *J. Anim. Sci.* 58:113-121.
- Hess, C. W. 1962. Randombred populations of the Southern Regional Poultry Breeding Project. *World's Poult. Sci. J.* 18:147-152.
- Hill, J. B. 1965. Automated fluorometric method for determination of serum calcium. *Clin. Chem.* 11:122-130.
- Johnson, D. H., and R. Thompson. 1995. Restricted maximum likelihood estimation of variance components of univariate models using sparse matrix techniques and average information. *J. Dairy Sci.* 78:423-447.
- Kornegay, E. T. 1996. Nutritional, environmental and economic considerations for using phytase in pig and poultry diets. Pages 277-302 in *Nutrient Management of Food Animals to Enhance and Protect the Environment*. E. T. Kornegay, ed. CRC Press, Boca Raton, FL.

- Latta, M., and M. Eskim. 1980. The simple and rapid calorimetry method for phytate determination. *J. Agric. Food Chem.* 26:1313-1315.
- Liu, J., D. W. Bollinger, D. R. Ledoux, and T. I. Veum. 1998. Lowering the dietary calcium to phosphorus ratio increases phosphorus utilization in low phosphorus corn-soybean meal diets supplemented with microbial phytase for growing finishing pigs. *J. Anim. Sci.* 76:808-813.
- Marks, H. L. 1991. Feed efficiency changes accompanying selection for body weight in chickens and quail. *World's Poult. Sci. J.* 47:197-212.
- McCarthy, J. C., and P. B. Siegel. 1983. A review of genetic and physiological effects of selection in meat-type poultry. *Anim. Breed. Abstr.* 51:88-95.
- Mohammed, A., M. J. Gibney, and T. G. Taylor. 1991. The effects of dietary levels of inorganic phosphorus, calcium and cholecalciferol on the digestion of phytate phosphorus by the chick. *Br. J. Nutr.* 66:251-259.
- Mrode, R. A. 1996. *Linear Models for the Prediction of Animal Breeding Values.* CAB Int., Wallingford, UK.
- Nelson, T. S. 1967. The utilization of phytate phosphorus by poultry: A review. *Poult. Sci.* 46:862-871.
- Punna, S., and D. A. Roland. 1999. Variation in phytate phosphorus utilization within the same broiler strain. *J. Appl. Poult. Res.* 8:10-15.
- Quaas, R. L. 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. *Biometrics* 32:949-953.
- Ravindran, V., W. L. Bryden, and E. T. Kornegay. 1995. Phytates: Occurrence, bioavailability, and implications in poultry nutrition. *Poult. Avian Biol. Rev.* 6:125-143.
- Sandberg, A.-S., T. Larsen, and B. Sandsrom. 1993. High dietary calcium level decreases colonic phytate degradation in pigs fed a rapeseed diet. *J. Nutr.* 123:559-566.
- SAS Institute. 1998. *SAS User's Guide.* Version 8.12. SAS Inst. Inc., Cary, NC.
- Sebastian, S., S. P. Touchburn, E. R. Chavez, and P. C. Lague. 1996. The effects of supplemental microbial phytase on the performance and utilization of dietary calcium, phosphorus, copper and zinc in broiler chickens fed corn-soybean diets. *Poult. Sci.* 75:725-736.
- Sharpley, A., J. J. Meisinger, A. Breeuwsma, J. T. Sims, T. C. Daniel, and J. S. Scheepers. 1998. Impact of animal manure management on ground and surface water quality. Pages 173-242 in *Animal Waste Utilization: Effective Use of Manure as a Soil Resource.* J. L. Hatfield, and B. A. Stewart, ed. Ann Arbor Press, Boca Raton, FL.
- Shirley, R. B., and H. M. Edwards Jr. 2003. Graded levels of phytase past industry standards improve broiler performance. *Poult. Sci.* 82:671-680.
- Smith, T. N., G. M. Pesti, R. I. Bakalli, J. Kilburn, and H. M. Edwards. 2001. The use of near-infrared reflectance spectroscopy to predict the moisture, nitrogen, calcium, total phosphorus, gross energy, and phytate phosphorus contents of broiler excreta. *Poult. Sci.* 80:314-319.
- Stuard, A., and J. K. Ord. 1994. *Kendall's Advanced Theory of Statistics.* Vol. 1: Distribution Theory. 6th ed. Halsted Press, New York, NY.
- Underwood, E. J., and N. F. Suttle. 1999. *The Mineral Nutrition of Livestock.* 3rd ed. CAB Int., Wallingford. Oxon, UK.
- US Environmental Protection Agency. 1990. *Nonpoint Sources Agenda for the Future.* Publ. WH-556. Office of Water, Washington, DC.
- Zhang, W., S. E. Aggrey, G. M. Pesti, R. I. Bakalli, and H. M. Edwards Jr. 2005a. Genetic analysis on the direct response to divergent selection for phytate phosphorus bioavailability in a randombred chicken population. *Poult. Sci.* 84:370-375.
- Zhang, W., S. E. Aggrey, G. M. Pesti, R. I. Bakalli, and H. M. Edwards Jr. 2005b. Correlated responses to divergent selection for phytate phosphorus bioavailability in a randombred chicken population. *Poult. Sci.* 84:536-542.
- Zhang, W., S. E. Aggrey, G. M. Pesti, H. M. Edwards, and R. I. Bakalli. 2003. Genetics of phytate phosphorus bioavailability: Heritability and genetic correlations with growth and feed utilization traits in randombred chicken population. *Poult. Sci.* 82:1075-1079.