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Comparative evaluation of mathematical functions to describe growth and efficiency of phosphorus utilization in growing pigs

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ABSTRACT: Success of pig production depends on maximizing return over feed costs and addressing potential nutrient pollution to the environment. Mathematical modeling has been used to describe many important aspects of inputs and outputs of pork production. This study was undertaken to compare 4 mathematical functions for the best fit in terms of describing specific data sets on pig growth and, in a separate experiment, to compare these 4 functions for describing of P utilization for growth. Two data sets with growth data were used to conduct growth analysis and another data set was used for P efficiency analysis. All data sets were constructed from independent trials that measured BW, age, and intake. Four growth functions representing diminishing returns (monomolecular), sigmoidal with a fixed point of inflection (Gompertz), and sigmoidal with a variable point of inflection (Richards and von Bertalanffy) were used. Meta-analysis of the data was conducted to identify the most appropriate functions for growth and P utilization. Based on Bayesian information criteria, the Richards equation described the BW vs. age data best. The additional parameter of the Richards equation was necessary because the data required a lower point of inflection (138 d) than the Gompertz, with a fixed point of inflexion at 1/e times the final BW (189 d), could accommodate. Lack of flexibility in the Gompertz equation was a limitation to accurate prediction. The monomolecular equation was best at determining efficiencies of P utilization for BW gain compared with the sigmoidal functions. The parameter estimate for the rate constant in all functions decreased as available P intake increased. Average efficiencies during different stages of growth were calculated and offer insight into targeting stages where high feed (nutrient) input is required and when adjustments are needed to accommodate the loss of efficiency and the reduction of potential pollution problems. It is recommended that the Richards and monomolecular equations be included in future growth and nutrient efficiency analyses.

Key words: function, growth, phosphorus, pig

INTRODUCTION

Traditionally, growth functions have been used to describe increase in BW over time. One of the outputs of generating growth curves is to have the ability to predict accurately the time at which pigs will be ready for market. A useful growth function should describe data well and contain biologically and physically meaningful parameters (France et al., 1996). Protein accretion (Ferguson et al., 1994), BW (Bridges et al., 1992), and mineral deposition (Mahan and Shields, 1998) are among attributes to be quantified using growth functions. In swine nutrition, Schinckel and de Lange (1996) identified protein accretion, partitioning of energy, maintenance requirement, and feed intake as primary requirements in developing growth models. Growth functions can be grouped into 3 categories: those that represent diminishing returns behavior (e.g., monomolecular), sigmoidal behavior with a fixed point of inflection (e.g., Gompertz, logistic), and those encompassing sigmoidal behavior with a flexible point of inflection (e.g., Richards, von Bertalanffy). The flexible functions are often generalized models that encompass simpler...
models for particular values of certain additional parameters. Although the Gompertz has been applied widely, other functions have been used to describe growth in nonruminant animals (e.g., Darmani Kuhi et al., 2003b).

Another application of growth curves is to relate BW to cumulative nutrient intake. It is useful to examine intake in order to assess genetic improvements (Bermudo et al., 2003) or to increase return over feed costs. Phosphorus is an essential nutrient that has received attention for environmental reasons such as limited supply and pollution of ponds and streams (Schulin-Zeuthen et al., 2005). Therefore, optimizing of P intake and understanding factors affecting P utilization in pigs have environmental and economic benefits. Growth functions can be used to determine efficiency of nutrient utilization (Darmani Kuhi et al., 2003a), which is the derivative of the relationship between BW and cumulative nutrient intake.

The aim of this study was to evaluate 4 candidate mathematical functions for best fit in describing specific data sets on pig growth, and to evaluate these 4 functions for describing of P utilization for growth in a separate experiment.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from existing databases (Table 1).

Data Sources

A total of 2,450 observations from 102 pigs originating from 3 independent data sets (Table 1) were used in this study. All 3 data sets had data on individual pigs and were derived from experiments conducted in Denmark, Spain, and Canada. Separate analyses were undertaken to relate BW to time and BW to cumulative P intake. Data sets 1 and 2 were used for growth analysis, and data set 3 for P efficiency analysis.

Growth Analysis. Two data sets with a total of 1,120 observations from 48 pigs were used to compare 4 equations to describe growth in pigs. Data set 1 consisted of birth to maturity records from 5 castrated, 5 male, and 5 female pigs. The pigs were crossbred \( \frac{1}{4} \) Danish Landrace, \( \frac{1}{4} \) Yorkshire, and \( \frac{1}{2} \) Duroc. Individual BW was recorded weekly and feed intake twice weekly. All pigs received 7 diets (based on barley and soybean) during their life span to maximize growth based on Danish standards (Table 1). The pigs were raised between 1996 and 2001 (Schulin-Zeuthen, 2000; Schulin-Zeuthen and Danfær, 2001).

Data set 2 consisted of data collected from 33 Spanish grower-finisher pigs (25 to 140 kg) of 2 sexes (females and castrated males) with BW and feed intake recorded every third week. The pigs were crossbred \( \frac{1}{4} \) Danish Landrace, \( \frac{1}{4} \) Yorkshire, and \( \frac{1}{2} \) Duroc. Individual BW was recorded weekly and feed intake twice weekly. All pigs received 7 diets (based on barley and soybean) during their life span to maximize growth based on Danish standards (Table 1). The pigs were raised between 1996 and 2001 (Schulin-Zeuthen, 2000; Schulin-Zeuthen and Danfær, 2001).

Data set 2 consisted of data collected from 33 Spanish grower-finisher pigs (25 to 140 kg) of 2 sexes (females and castrated males) with BW and feed intake recorded every third week. The pigs were crossbred \( \frac{1}{4} \) Large White, \( \frac{1}{4} \) Landrace, and \( \frac{1}{2} \) Large White or Pietrain. They received a grower and a finisher diet, based on corn (32.6 and 28.5%), soybean meal (24.5 and 21%), barley (10 and 15%), and wheat (10 and 10%) for grower
and finisher diets, respectively (Tibau et al., 2002; Jondreville et al., 2004; Table 1).

**Phosphorus Efficiency Analysis.** Data set 3 with 1,330 observations was used to test the fit of 4 functions to describe efficiency of P utilization in growing pigs. An experiment using 54 Yorkshire pigs (30 males and 24 females), with an initial BW of 25 kg conducted at the University of Guelph (Swidersky et al., 2003), was used to construct data set 3. The pigs were randomly assigned to 1 of the 4 dietary P levels. The treatments were low, medium, recommended, and high available P intakes corresponding to 52, 78, 105 and 130%, respectively, of the NRC (1998) requirements for grower and finisher pigs. Pigs had ad libitum access to feed and feed intake was recorded automatically. For individual pigs housed in groups, 2 diets were prepared for grower and finisher phases, based on corn (73.1 and 80%) and soybean meal (24.0 and 17.3%; Swidersky et al., 2003; Table 1). The data set was selected because of the wide range of P intakes. The 4 functions can also describe Ca efficiency, as Ca was varied in tandem with P because of their close association; however, the diets were formulated to be first-limiting in P.

**Mathematical Models**

**Growth Analysis.** The growth equations chosen in the study represent diminishing returns behavior (monomolecular), sigmoidal with a fixed point of inflection (Gompertz), and sigmoidal with a variable point of inflection (von Bertalanffy and Richards) as described in Chapter 5 of Thornley and France (2007).

The monomolecular equation, the simplest equation used in this study, was used in the following form with 3 parameters:

\[
W = W_f - (W_f - W_0)e^{-kt},
\]

where \(W\) is BW (kg) at age \(t\) (d), \(W_0\) is initial BW at birth (\(t = 0\)), \(W_f\) is asymptotic BW reached as \(t \to \infty\), and \(k\) is a rate constant (d\(^{-1}\)). The monomolecular equation describes the progress of a simple, irreversible first-order reaction.

The Gompertz equation can be derived by assuming substrate (feed) is nonlimiting, the quantity of growth machinery is proportional to \(W\), and effectiveness of the growth machinery decays exponentially with time according to a decay constant \(k\) (d\(^{-1}\)). The Gompertz equation was used in the following form:

\[
W = W_0 \exp \left[\ln \frac{W_f}{W_0} (1 - e^{-kt})\right].
\]

Inflection in this sigmoidal growth function occurs at \(W = W_f/e\).

In the von Bertalanffy equation, the assumptions are that the substrate is nonlimiting, and the growth process is the difference between anabolism and catabolism. The form of the von Bertalanffy used in this study was

\[
W = [W_f^\gamma - (W_f^\gamma - W_0^\gamma)e^{-k\gamma}]^{1/n},
\]

where \(n\) (dimensionless, with bounds \(0 < n \leq 1/3\)) and \(k\) (d\(^{-1}\)) are parameters. Inflection occurs at \(W = (1 - n)^{1/n}W_f\).

The Richards equation is an empirical construct and therefore does not have the underlying biological basis of the previous models. However, it belongs in the same group of classic growth models, and its flexibility, due to its shape parameter \(n\) (dimensionless), makes it a generalized alternative to other equations (e.g., those with fixed inflection points such as the Gompertz). The Richards equation was used in the following form:

\[
W = \frac{W_0W_f}{(W_0^\gamma + (W_f^\gamma - W_0^\gamma)e^{-k\gamma})^{1/n}}
\]

where \(k\) (d\(^{-1}\)) is a positive constant, and \(n\) is \(\geq -1\) to ensure physiological growth rates as \(W \to 0\). Inflection occurs, provided \(n\) is \(> -1\), at \(W = W_f [1/(n + 1)]^{1/n}\).

**Phosphorus Efficiency Analysis.** Growth equations can also be used to obtain parameters describing conversion of intake (e.g., feed, P, or other nutrient) to animal products such as BW. Data set 3 contains data with different levels of P and Ca intake but similar intake of other nutrients, so the equations can be tested for their ability to determine values of efficiency of P utilization. To describe efficiency, BW needs to be expressed in terms of intake. In this analysis BW, \(W\) (kg) was regressed against cumulative intake of available P, \(P\) (g), and the models described above, with age replaced by cumulative intake, were evaluated for their ability to determine the efficiency of P utilization.

The instantaneous efficiency of P utilization for gain, \(k_P\) (kg of BW/g of P), is given by differentiating the \(W\) vs. \(P\) relationship:

\[
k_P = \frac{dW}{dP},
\]

and the average efficiency of utilization of P for gain (\(\bar{k}_P\)) between 2 P intake levels \(P_1\) and \(P_2\) is

\[
\bar{k}_P = \frac{P_2}{P_2 - P_1} \cdot \frac{\int dW}{\int dP} = \frac{P_2}{P_2 - P_1} \cdot \frac{w_2}{w_1} = \frac{(W_2 - W_1)}{(P_2 - P_1)}.
\]

**Statistical Procedures**

**Growth Analysis.** The 4 models described were fitted to the 2 data sets combined using the nonlinear mixed procedure (PROC NL MIXED, Littell et al., 1996; SAS Inst. Inc., Cary, NC). Mixed model analysis was chosen because the data were gathered from various studies; therefore, it was necessary to consider analyzing not only fixed effects of the dependent variable but also random effects (because the studies represent a random sample of a larger population of studies). For
this analysis, a nonlinear mixed procedure based on Craig and Schinckel (2001) and Schinckel and Craig (2002) was employed. Forward selection was used to find the optimum model with lowest value of Bayesian information criterion (BIC; Leonard and Hsu, 2001). Trial was coded as a random effect, and between-pig variability was modeled by introducing a parameter ($c$) to vary the mature BW, which was also a random effect (Craig and Schinckel, 2001). For example, for the monomolecular equation, the model fitted was $W = (c + \mu) \times \left[ W_f - (W_f - W_0)e^{-k}t \right]$, where $\mu$ is the random effect of each pig. Introducing sex as a fixed source of variation in the model did not improve the performance of the models because most of the variability associated with differences in sex had been explained by the between-pig variability parameter.

**Phosphorus Efficiency Analysis.** Nonlinear mixed model analysis was also used in determining efficiency of P utilization. First, the equations were fitted to the data, and then derivatives of the growth curves were calculated. In fitting the equations, the fixed effects of available P intake level and sex were considered. The NLMIXED procedure of SAS does not support directly the concept of an independent discrete (class) variable, so the analysis was performed using dummy variables to represent treatments, sex, or both. Each parameter was considered individually at first, and then a combination of parameters was used. Model comparison using an $F$-test showed that the rate parameter ($k$) was significantly affected by treatment ($P < 0.01$) and inclusion of other parameters did not improve the overall model performance. Therefore, the model with separate $k$ values but a common $W_0$, $W_f$, and $n$ was fitted.

Distribution of random effects was assumed to be normal and the dual quasi-Newton technique was used for optimization with adaptive Gaussian quadrature as the integration method. Performance of the models was evaluated using the significance level of the parameters estimated, the variance of error estimate, and its approximate SE. Comparison of models was based on BIC, which are model-order selection criteria centered on parsimony and imposing a penalty on more complicated models for inclusion of additional parameters. Bayesian information criterion combines the maximum likelihood (data fitting) and the choice of model by penalizing the (log) maximum likelihood with a term related to model complexity, as follows: BIC = $-2 \log(\hat{J}) + K\log(N)$, where $\hat{J}$ is the maximum likelihood, $K$ is number of free parameters in the model, and $N$ is sample size. A smaller numerical value of BIC indicates a better fit when comparing models.

Both analyses were performed with the assumption that variance distribution for the fixed factor was normal. Random effects were assumed to be normally distributed.

**RESULTS**

**Growth Analysis**

In general, all the equations fitted BW vs. age data well below approximately 350 kg (Figure 1). The nonlinear analysis of the pooled data sets showed that $W_0$ estimates were close to zero for all of the models compared. The estimate of $W_0$ from the monomolecular equation was greatest compared with the other equations. The von Bertalanffy equation estimated $W_0$ to be decreased compared with the other equations (Table 2). Estimates of $W_f$ were within a 0.07-kg range for the sigmoidal equations. More importantly, the random effect multiplier based on BW, ($c$), was also within a narrow range. Due to the introduction of a random effect of between-pig variation, the parameter estimate of mature pig BW ($W_f$) as described above is not absolute. Therefore, to aid comparison between models, the estimated mature BW was calculated by multiplying $W_f$ and $c$ (Table 2) with the monomolecular and Gompertz equations showing greatest and the lowest estimates, respectively. The rate constant parameter estimates ($k$) ranged between 0.0028 and 0.0067, and were significantly different from zero for all models. Finally, the parameter $n$ estimates were $-0.40$ and $0.33$ for Richards and von Bertalanffy equations, respectively.

Comparison of models based on BIC suggested an advantage in using a more complex model (Richards) compared with simpler models such as the Gompertz or monomolecular. The von Bertalanffy equation also appeared to improve predictions (Figure 1) compared with the monomolecular equation. However, the addition of an extra parameter in the von Bertalanffy equation did not result in significant improvement in goodness-of-fit with this model compared with the Gompertz equation, as reflected by their similar BIC values.

**Phosphorus Efficiency Analysis**

Cumulative available dietary P intake was calculated from feed intake measurements and corresponding available P content of the diet. For a given BW, the amount of available P consumed up to that particular time was entered in the database.

Fitting the equations to plots of BW vs. cumulative available dietary P intake (Figure 2) showed that the parameter estimate for initial BW at zero P intake ranged from 19.2 for the monomolecular equation to 28.7 kg for Richards equation (Table 3). Final BW estimates ranged from 131.9 (Richards) to 193.3 kg (monomolecular). All initial and final BW estimates for all 4 models were significant parameters in the model. Rate constant estimates ranged from 0.0028 to 0.0067; $n$ parameter estimates were $-0.87$ and $0.33$ for the Richards and von Bertalanffy equations, respectively.

The model with separate rate constant values for each treatment category significantly improved on the general model in all equations compared. However, comparisons of the models using $t$-tests of parameter values failed to reject the null hypothesis that BW gain was not significantly different between sexes ($P > 0.05$). Animals fed high levels of available P showed the lowest estimates of rate constants, which increased as the lev-
els of available P decreased. In all models, the differences in the estimate of rate constants among dietary P levels were significant (Table 3).

Comparison of models based on BIC did not show any advantage in using a more complex equation than the monomolecular (Table 3). The 3 sigmoidal equations did not do as well as the monomolecular equation, but their BIC values were within a narrow range. The Richards equation was marginally improved compared with the other sigmoidal equations, and its parameter estimates were close to those of the monomolecular equation, with a point of inflection at a very small BW over the range of cumulative P intake. The Gompertz and von Bertalanffy equations were the least suitable for analyzing efficiency of P utilization.

Calculations of maximum efficiency of P utilization showed wide variation between models. Maximum efficiency was at a considerably lower BW for Richards (8.0 kg) than for von Bertalanffy (56.5 kg) and Gompertz (57.9 kg) equations. The monomolecular equation as-

Table 2. Parameter estimates and SE obtained by nonlinear regression of BW vs. age (data sets 1 and 2)

<table>
<thead>
<tr>
<th>Item</th>
<th>Monomolecular</th>
<th>Gompertz</th>
<th>Richards</th>
<th>von Bertalanffy</th>
</tr>
</thead>
<tbody>
<tr>
<td>$W_0$, kg</td>
<td>0.05</td>
<td>0.009</td>
<td>0.01</td>
<td>0.030</td>
</tr>
<tr>
<td>$W_f$, kg</td>
<td>19.5</td>
<td>0.45</td>
<td>&lt;0.001</td>
<td>1.01</td>
</tr>
<tr>
<td>$c$</td>
<td>21.9</td>
<td>0.501</td>
<td>0.021</td>
<td>378</td>
</tr>
<tr>
<td>$W_f \times c$, kg</td>
<td>427</td>
<td>382</td>
<td>394</td>
<td>389</td>
</tr>
<tr>
<td>$k$, d$^{-1}$</td>
<td>0.0028</td>
<td>0.0001</td>
<td>&lt;0.001</td>
<td>0.0067</td>
</tr>
<tr>
<td>$n$</td>
<td>226</td>
<td>9.97</td>
<td>0.021</td>
<td>190</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>8,872</td>
<td>8,744</td>
<td>8,726</td>
<td>8,745</td>
</tr>
<tr>
<td>BIC</td>
<td>8,872</td>
<td>8,744</td>
<td>8,726</td>
<td>8,745</td>
</tr>
<tr>
<td>Calculated growth trait</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$t^*$</td>
<td>NA</td>
<td>189</td>
<td>138</td>
<td>158</td>
</tr>
<tr>
<td>$W^*$</td>
<td>NA</td>
<td>139</td>
<td>91.7</td>
<td>110</td>
</tr>
</tbody>
</table>

1$W_0$ is initial BW at $t = 0$, $W_f$ is asymptotic mature BW, $c$ a parameter to estimate between-pig variability of mature BW, $k$ is a rate constant, $n$ is a shape parameter influencing point of inflection, $\sigma$ is SE of model (= variance ($\sigma^2$) of error), BIC (Bayesian information criterion) is a measure of regression fit, and $t^*$ and $W^*$ are age and BW at the inflection point, respectively.
Figure 2. Relationship between BW (kg) and cumulative available phosphorus intake (g) in Data set 3. Symbols represent observed values (circle, square, triangle, and inverted triangle correspond to treatments with available P intakes of 52, 78, 105, and 130% of the NRC (1998) recommendation, respectively), and the lines are regression lines fitted using the 4 candidate equations.

The growth curve was divided into 4 phases as shown in Figure 3. The lag phase was defined as time from the initial BW estimate until the animal attains 10% of its final BW, the accelerating phase continues from the end of lag phase until maximum growth rate (point of inflection) is achieved, then the animal goes into the

Table 3. Parameter estimates and SE obtained by nonlinear regression of BW vs. cumulative P intake (data set 3)

<table>
<thead>
<tr>
<th>Item</th>
<th>Monomolecular</th>
<th></th>
<th></th>
<th>Gompertz</th>
<th></th>
<th></th>
<th>Richards</th>
<th></th>
<th></th>
<th>von Bertalanffy</th>
<th></th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
<td>P-value</td>
<td>Estimate</td>
<td>SE</td>
<td>P-value</td>
<td>Estimate</td>
<td>SE</td>
<td>P-value</td>
<td>Estimate</td>
<td>SE</td>
<td>P-value</td>
</tr>
<tr>
<td>$W_0$, kg</td>
<td>19.2</td>
<td>2.14</td>
<td>&lt;0.001</td>
<td>27.5</td>
<td>0.34</td>
<td>&lt;0.001</td>
<td>28.7</td>
<td>0.97</td>
<td>&lt;0.001</td>
<td>27.0</td>
<td>0.36</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$W_f$, kg</td>
<td>193</td>
<td>5.26</td>
<td>&lt;0.001</td>
<td>157</td>
<td>3.04</td>
<td>&lt;0.001</td>
<td>132</td>
<td>7.26</td>
<td>&lt;0.001</td>
<td>178</td>
<td>4.71</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$k_1$, g(^{-1})</td>
<td>0.0038</td>
<td>0.0015</td>
<td>&lt;0.001</td>
<td>0.0082</td>
<td>0.0022</td>
<td>&lt;0.001</td>
<td>0.0031</td>
<td>0.0017</td>
<td>&lt;0.001</td>
<td>0.0071</td>
<td>0.0021</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$k_2$, g(^{-1})</td>
<td>0.0025</td>
<td>0.0010</td>
<td>&lt;0.001</td>
<td>0.0055</td>
<td>0.0015</td>
<td>&lt;0.001</td>
<td>0.0020</td>
<td>0.0016</td>
<td>&lt;0.001</td>
<td>0.0040</td>
<td>0.0014</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$k_3$, g(^{-1})</td>
<td>0.0019</td>
<td>0.0008</td>
<td>&lt;0.001</td>
<td>0.0041</td>
<td>0.0011</td>
<td>&lt;0.001</td>
<td>0.0014</td>
<td>0.0010</td>
<td>&lt;0.001</td>
<td>0.0030</td>
<td>0.0011</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$k_4$, g(^{-1})</td>
<td>0.0013</td>
<td>0.0005</td>
<td>&lt;0.001</td>
<td>0.0027</td>
<td>0.0007</td>
<td>&lt;0.001</td>
<td>0.0009</td>
<td>0.0008</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>20.5</td>
<td>0.34</td>
<td>&lt;0.001</td>
<td>25.6</td>
<td>0.25</td>
<td>&lt;0.001</td>
<td>25.3</td>
<td>0.21</td>
<td>&lt;0.001</td>
<td>25.9</td>
<td>0.64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BIC</td>
<td>7,557</td>
<td></td>
<td></td>
<td>7,667</td>
<td></td>
<td></td>
<td>7,666</td>
<td></td>
<td></td>
<td>7,671</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Calculated growth trait:

- $t_1$ is initial BW at $t = 0$.
- $W_f$ is asymptotic mature BW.
- $k$ is a rate constant.
- $n$ is a shape parameter influencing point of inflection.
- $\sigma$ is SE of model (\(= \sqrt{\text{variance (SE)}^2}\) of error).
- BIC (Bayesian Information Criterion) is a measure of regression fit.
- $t_i$ and $W_i$ are available P intakes (g) and BW (kg) at the inflection points, respectively.

Subscript numbers for $k$ and $t$ denote treatments with P levels of 52, 78, 105, and 130% of the NRC (1998), respectively.

\(^1\)W0 is initial BW at t = 0, Wf is asymptotic mature BW, k is a rate constant, n is a shape parameter influencing point of inflection, \(\sigma\) is SE of model (= \text{variance (SE)}^2 of error), BIC (Bayesian Information Criterion) is a measure of regression fit, and $t_i$ and $W_i$ are available P intakes (g) and BW (kg) at the inflection points, respectively. Subscript numbers for $k$ and $t$ denote treatments with P levels of 52, 78, 105, and 130% of the NRC (1998), respectively.
Figure 3. Growth stages for a representative sigmoidal curve and graphical representation of instantaneous efficiency for the monomolecular equation. $W_0$ is initial BW at time, $t = 0$, $W_f$ is final BW when $t \to \infty$, $W_l$ is BW at the end of the lag phase (calculated as $W_0 + 0.1W_f$), $W^*$ is BW at inflection, $W_d = 0.9W_f$, and $k_P$ is instantaneous efficiency of phosphorus utilization for growth.

deceleration phase until it reaches 90% of its mature BW, and finally into the stationary phase that continues until the approach of asymptotic final BW. Figure 3 also depicts graphically instantaneous efficiency of P utilization taking the monomolecular equation as an example.

Average efficiency of P utilization for gain in the stages described above is given in Table 4. The calculations were made by taking into account the significant differences in the rate constant. Averages from 25 to 100 kg, 25 to 50 kg, and 50 to 100 kg (BW intervals covering the growing-finishing periods) are also given because these could have implications for commercial production systems. As expected, the greatest average BW gain and efficiency of P utilization for the monomolecular equation was during the first phase, whereas for the Gompertz and von Bertalanffy equations, greatest BW gain was during the acceleration phase. For all the equations, P efficiency approaches zero in the stationary phase.

DISCUSSION

Weight gain has been described using growth equations, and in nonruminants, the Gompertz has traditionally been the model of choice (Wellock et al., 2004). In this study, a simpler model (monomolecular) and others without the limitation of a fixed point of inflection (which occurs at 1/e times the final BW in the Gompertz), such as Richards and von Bertalanffy equations, were evaluated. The analyses showed that, in general, all 4 growth equations fitted the data reasonably well (Figures 1 and 2).

Performance of the equations in describing the data sets was evaluated using BIC, which suggested differences in model choice for growth in BW and efficiency of P utilization. A notable difference in parameter estimates in both sets of analyses was for $W_0$. Estimates of $W_0$ were lower in the growth analysis because the data contained information on birth weights whereas birth weight data were not available for the P efficiency analysis. The $W_0$ estimates were within the range of 0.042 and 9.5 kg in the first and second analyses, respectively. The $W_f$ estimates in growth analysis have to be looked at in conjunction with the $c$ parameter, which was within 18 kg for the sigmoidal curves. The introduction of random effect of mature BW increased the goodness-of-fit (lower BIC value) compared with a generalized model with only experiment as the random element in the model. It has also improved the approximate SE of the parameter estimates.

Comparison of BIC values for the growth analysis revealed that the Richards equation, perhaps due to the broad limits on its additional parameter, was superior to the other equations. As parameter $n$ approaches particular values, the Richards equation encompasses other simpler models, such as the monomolecular ($n = -1$), Gompertz ($n = 0$), and logistic ($n = 1$). Table 2 shows that $n$ estimate was about halfway between the monomolecular and Gompertz equations. The flexibility of the Richards equation increased the accuracy of prediction, and the need for an additional parameter was justified because the shape of the curve could not be described as well by the monomolecular (because it is not a sigmoidal equation) or the Gompertz (due to its fixed inflection point).

Four phases were arbitrarily assigned to evaluate BW gain (Figure 3), and the average efficiency of BW gain with time within the phases was calculated. The values based on generalized sigmoidal equations were close to each other but different from those based on the monomolecular equation. The importance of this kind of calculation is to identify periods of greatest BW gain so that inputs can be adjusted accordingly. More crucially, by recognizing the rate of decline in growth during the stationary phase, more informed decisions can be made about the impact of varying slaughter weight on nutrient use and income over diet costs. From
the Richards equation, it can be calculated that the pigs were expected to gain nearly 1 kg/d during the accelerating phase, which goes down by about 40% in the next phase; by the time they reach the stationary phase, the animals were 97% less efficient in gaining BW. The data also show that there was uniformity up to the end of the accelerating phase (d 300 of age); then, as animals matured, there were greater differences among animals due to the BW gains being mainly attributable to fat deposition.

Apart from describing the pattern of growth, nonlinear equations can be used to investigate efficiency of utilization of individual nutrients for BW gain. Usually, mineral requirements in pigs are estimated by empirical methods based on feeding a range of dietary concentrations of each mineral element and examining the response in terms of certain performance (BW gain) or physiological (mineral balance) attributes to assess the most adequate dietary concentration (i.e., the one resulting in maximum response). In general, as P intake is increased, there is an increase in BW gain, feed intake, and feed efficiency (gain to feed ratio); this relationship is curvilinear, such that maximum response is reached at a certain level of P intake, which is variable depending upon animal characteristics (genotype, sex) and the growing stage (Ketaren et al., 1993; Ekpe et al., 2002; Hastad et al., 2004). The response is less pronounced as the animal grows; hence in animals of greater BW the level of P intake required to reach the maximum response is lower (Ketaren et al., 1993; Hastad et al., 2004). From this approach, requirements have been mostly expressed as percentage of the mineral in the diet (or alternatively per unit of energy in the diet; ARC, 1981). However, in order to assess optimal requirements for a given growth rate, it is important to express requirements of P (and any other mineral) directly in relation to protein and fat gain, but this goal cannot be achieved with the information currently available in the literature.

Alternatively, the use of nonlinear equations to describe the relationship between BW and cumulative available P intake can be used to estimate the efficiency of P utilization in terms of BW gain per unit of available P intake at any stage of growth, provided that other nutrients are not limiting expression of nutrient retention rates. Using this approach, 4 nonlinear equations were examined. The Richards equation seemed to yield as good a fit as the Gompertz, given the almost identical BIC values. However, in this case, the estimate of parameter n was close to −1 (Table 3), approaching diminishing returns behavior without a point of inflection, so that the simple monomolecular equation was adequate to describe the relationship between BW and cumulative available P intake in pigs, which is confirmed by the lowest BIC value of the model. Most of the rate parameter estimates of the Richards and monomolecular equations were not significantly different from each other, which further proves the flexibility of the Richards equation and the suitability of the monomolecular equation to fit these profiles, without the need for an additional parameter. The same equation (Richards) can be used for both growth analysis and efficiency of nutrient utilization, and can yield different growth patterns for each of the 4 dietary P levels. Therefore, only 1 equation is required for all levels to assess the optimum level.

Calculations for efficiency of P utilization based on the best performing model (monomolecular equation) showed that the average efficiency is greatest during the 2 initial phases and slows down as the pig’s cumulative consumption of available P increases. By the time the pig reaches the stationary phase, efficiency approaches zero. This trend is the same in pigs fed low or high levels of P (Table 4). The steady decline in

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### Table 4. Calculated average efficiency of available P utilization in various stages of growth based on parameter estimates for the 4 candidate equations

<table>
<thead>
<tr>
<th>Equation</th>
<th>$k_{W^f}$</th>
<th>$k_{W^e}$</th>
<th>$k_{W^e-W^d}$</th>
<th>$k_{W^d-W^f}$</th>
<th>$k_{W^d-W^i}$</th>
<th>$k_{W^i-W^f}$</th>
<th>$k_{W^f-W^i}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Von Bertalanffy</td>
<td>0.62</td>
<td>0.53</td>
<td>0.22</td>
<td>0.014</td>
<td>0.59</td>
<td>0.44</td>
<td>0.48</td>
</tr>
<tr>
<td>Gompertz</td>
<td>0.43</td>
<td>0.47</td>
<td>0.31</td>
<td>0.035</td>
<td>0.43</td>
<td>0.44</td>
<td>0.44</td>
</tr>
<tr>
<td>Richards</td>
<td>0.50</td>
<td>0.47</td>
<td>0.32</td>
<td>0.039</td>
<td>0.39</td>
<td>0.45</td>
<td>0.43</td>
</tr>
<tr>
<td>Richards</td>
<td>0.45</td>
<td>0.47</td>
<td>0.28</td>
<td>0.020</td>
<td>0.45</td>
<td>0.44</td>
<td>0.44</td>
</tr>
</tbody>
</table>

1Two of the 4 rate constants ($k$) for treatments with the greatest ($k_1$) and lowest ($k_4$) available P intake levels are shown for comparison of efficiencies.

2$W_0$ is initial BW at time $t = 0$, $W_f$ is final BW when $t \to \infty$, $W_i$ is BW at end of lag phase (calculated as $0.1W_f + W_d$), $W^* = BW$ at inflection, $W_d = 0.9W_f$, and $k$ denotes average efficiency. For the monomolecular and for Richards equations (for P intake only), $W^*$ was calculated as $(W_f - W_l)/2$ because of the absence of the inflection point for the former and low value for the latter equation. The subscripted numbers appearing in the last 3 column headings are BW in kilograms.
efficiency of P utilization observed as a pig grows agrees with the lower P requirements recommended (ARC, 1981; NRC, 1998) for different growth phases (decreasing from weaning to 100 kg) and can be attributed to a number of reasons. The amount of P required for maintenance is greater in larger pigs, and thus relatively less P is used for growth (ARC, 1981; NRC, 1998). Also, it is important to examine variations in P deposition in the BW gain. Considering the principles of skeletal tissue growth, there is a steady and progressive increase in the rate of P accumulation per unit of fat-free BW from birth to slaughtering weight (Mahan and Shields, 1998). However, given the exponential increase in fat deposition in adipose tissue, the rate of increment of P content in empty BW is inversely related to BW, as demonstrated by Mudd et al. (1969) in trials using carcass analysis, reporting values of 8.1, 5.3, and 1.6 g of P/kg BW gain at 20, 50, and 90 kg of empty BW, respectively. Our analysis also shows that as BW increases, the proportion of P retained decreases. The ARC (1981) suggested that the rate of storage of Ca and P (g/kg of BW gain) with growth could be represented by a linear fall between birth and 50 kg of BW (with a linear relationship between that rate and BW) and a constant rate thereafter. Calculations of efficiency of P utilization as d(BW)/d(P intake) using nonlinear methods takes into account the relationship between BW and P as described by different classical growth equations. It is noteworthy that the levels of Ca and P resulting in maximum growth rate and efficiency of gain are not necessarily adequate for maximum growth mineralization (ARC, 1981). To achieve maximum deposition of Ca and P, and increase the bone mineral content, a greater mineral supply would be required (NRC, 1998; Hastad et al., 2004). The approach suggested herein could be used not only to quantify the trend in efficiency of P utilization throughout the life span of the animal, but also to examine differences between genotypes with different lean growth rate (Bertram et al., 1994) or but also to examine differences between genotypes with different lean growth rate (Bertram et al., 1994) or sex (comparison among gilts, barrows, or boars; Thomas and Kornegay, 1981; Ekpe et al., 2002). In a commercial environment. J. Anim. Sci. 82:2945–2952.


References

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