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► To cite this version:

Ludovic Brossard, Jean-Yves Dourmad, Florence Garcia-Launay, Jaap J. van Milgen. Modelling nutrient requirements for pigs to optimize feed efficiency. Achieving sustainable production of pig meat, 24, Burleigh Dodds Science Publishing Limited, pp.307, 2017, Burleigh Dodds Series in Agricultural Science, 978-1-78676-092-0. 10.19103/AS.2017.0013.10. hal-01644029

HAL Id: hal-01644029 https://hal.science/hal-01644029

Submitted on 21 Nov 2017

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Modelling nutrient requirements for pigs to optimise feed efficiency Ludovic Brossard, Jean-Yves Dourmad, Florence Garcia-Launay and Jaap van Milgen, INRA – Agrocampus Ouest, France

Abstract

Improvement of feed efficiency is crucial if pig production is to meet the challenge of sustainability in terms of production costs and environmental impact. This implies to precisely know the nutrient requirements of sows and growing pigs to develop adapted feeding strategies and thus optimize performance. This chapter describes existing modelling approaches developed to predict the nutrient requirement of a single individual animal (growing pig or sow) in terms of protein / amino acids, energy and minerals, and depending on characteristics of the pig and the feed, and environmental conditions. The chapter proposes and explains the integration of individual variability among animals into models for pig feeding, its application in precision feeding, and illustrates via a case study the relevance of the application of these models for improving feed efficiency.

Key words: Pig nutrition; Nutritional modelling; Pig nutrient requirements; Feed efficiency; Precision feeding

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1 Introduction

Animal production is continuously facing the challenge of sustainability. In the next decades, world animal production is expected to increase by about 70% to satisfy the increased demand for animal protein, as anticipated by FAO (2011). Meeting this

demand in a sustainable way requires increasing the efficiency of animal production. Additionally, livestock production systems have also to integrate the dimensions of animal health and welfare, food quality and security, environment, and consumer and citizen expectations to ensure their sustainability. In pig production, feed and feeding are major levers to control performance, with immediate and reversible effects. Feed represents a major part of the production costs (typically 60 to 70%) and thus largely affects economic results. Feed is also largely implicated in other sustainability pillars by its action on performance, animal welfare and health, product quality and environmental impact. For most nutrients, the efficiency with which animals transform dietary inputs to animal products is relatively low. For protein, this efficiency rarely exceeds 50%, while for phosphorus and energy these efficiencies are even lower. This implies that knowledge of nutritional requirements, combined with their availability in feed ingredients, is of major importance to develop feeding strategies that contribute to improving the feed efficiency.

The requirement of nutrients such as amino acids or minerals, when all other nutrients are provided at adequate levels, can be defined as the amount needed for specified production purposes such as growth, protein deposition, milk production or maintenance (Fuller, 2004). Nutrient requirements are affected by factors related to the animal (e.g. genetic, age, weight, sex, social status and health), the feed (e.g. feed allowance, nutrient composition and digestibility) and housing conditions (e.g. ambient temperature and space allowance) (Noblet and Quiniou, 1999). Two methods are generally used to determine the nutrient requirements of pigs: the empirical and the factorial methods (Patience et al., 1995). A comparison of these two methods has been given by Hauschild et al. (2010b) and Pomar et al. (2013). In the empirical approach, the requirement for a nutrient is determined by feeding groups of pigs with increasing levels of this nutrient while measuring one or several performance traits during a given time interval. With this method, the nutrient requirement corresponds to the population requirement for the considered performance and time interval. The estimated requirement may depend on the measured performance trait and on the statistical model used to estimate the population requirement (Pomar et al., 2013). Differences in pig characteristics (e.g. adiposity in growing pigs and prolificacy in sows), and the effect of the environment on the requirement limits the possibility of extrapolation of results

to other production situations (Pomar et al., 2003). It is why the factorial approach is generally preferred and considered as a reference method. With this method, the estimated nutrient requirement includes requirements for maintenance and production, and the efficiency of nutrient use (Fuller and Chamberlain, 1982; van Milgen and Noblet, 2003). Requirements are assumed to be the amount of the given nutrient that will allow the animal to perform normally its needed functions, without limiting growth (Pomar et al., 2013). As illustrated for lysine in Pomar et al. (2013), the requirement for a nutrient is calculated as the sum of lysine requirements for given functions (e.g. basal endogenous losses and daily gain) expressed as quantity required for the nutrient per unit of feed intake, body weight (BW) or daily gain. Whereas the empirical approach is used to obtain the requirement at a population level, the factorial approach allows estimating the requirement of an individual animal at a given stage. Applying the factorial method to determine the requirement of a population needs to account for variability among pigs in a population. Indeed, using the requirement of the average pig to feed a population of pigs implies that half of the population will get less nutrients than required and the performance of the population will be lower than expected (Pomar et al., 2003; Brossard et al., 2009; Hauschild et al., 2010b). An alternative is to use a lower nutrient efficiency for the population than for individuals (NRC, 2012) or to increase the requirement by a given percentage (van Milgen et al., 2008). However, defining the population requirement is difficult, depending on whether it is considered as the nutrient amount required to satisfy the average pig, the most demanding pigs or a given proportion of pigs.

Even if the factorial method allows for a more mechanistic determination of requirement for a given level of performance, its application is not straightforward because of the dependency of this performance level to pig characteristics, nutritional supply, housing conditions, and their interactions (Noblet et al., 2016). Modelling approaches based on the factorial approach have been developed since the 1970s to predict the response of growing pigs or sows to the nutrient supply. These models have been developed to simulate the performance of a single animal and can be used as decision support tools to assess the nutrient requirement and identify appropriate feeding strategies (e.g. van Milgen et al., 2008; NRC, 2012). However, between-animal variation has been shown to affect the population response, the efficiency of nutrient utilization and, consequently, the optimal nutrient supply for the population (Leclercq and Beaumont, 2000; Pomar et al., 2003; Brossard et al., 2009). Therefore, stochasticity has been introduced in models to deal with variability and to simulate responses of groups of pigs (e.g. Ferguson et al., 1997; Knap, 1999; Pomar et al., 2003; Vautier et al., 2013). These approaches have shown that variation among animals needs to be considered to improve nutrient efficiency on-farm. Assessing variation among animals is possible through the development of monitoring devices that allow one to characterize individual animals on-farm, and through the development of feeding devices that are controlled through real-time decision support tools.

In this chapter, we will present briefly the existing modelling approaches developed to predict nutrient requirements of a single individual (growing pig or sow) in terms of protein/amino acids, energy, and minerals. We will then present how variability among animals can be integrated in modelling nutrient requirements. We will also illustrate how these models can be used in the development of precision feeding systems that allow improvement of feed efficiency.

2 Modelling pig nutrient requirements

As described in introduction, the factorial approach allows defining requirements for a given level of performance in a given environment. However, this performance level depends on several factors such as pig characteristics (e.g. age, weight, sex, heath status and genetic potential), feeding level and feed quality, and housing conditions. Moreover, this method does not account for the possible interactions between these factors. Defining nutrient requirements more precisely implies to establish response curves between nutritional supplies and performance accordingly to the physiological status of the pig. Modelling approaches allow integrating these responses curves to predict performance (outputs from the model) from information on feed quantity and quality, animal characteristics, and housing conditions (inputs to the model) on the basis of a set of equations. Different types of models exists (France and Thornley, 1984; Sauvant, 2005). Empirical models, also called 'black box' models, relate inputs to outputs without relying on the underlying biological mechanisms. Mechanistic models include

underlying biological mechanisms to calculate outputs from inputs; this implies that these models are more complex and typically use numerous equations and parameters. Models predicting outputs at a given point in time or space are called static, which contrasts with dynamic models that describe the dynamic nature of the response over a given period (e.g. the fattening period). Finally, deterministic models have a fixed set of parameters and therefore do not account for variability among animals, the same set of parameter values for inputs implying the same values for outputs. In contrast, stochastic models integrate variability in model parameters, which offers the possibility to account for variation among animals in a population.

2.1 Growing pig models

Since the 1970s, different models, most of which are dynamic, deterministic, and more or less mechanistic, have been developed to simulate pig growth and to determine nutrient requirements. They are often based on the association of empirical equations and mechanistic description of physiological or biochemical functions of the animal. The concepts used in these models have been summarized and compared by several authors (Bastianelli and Sauvant, 1997; Ferguson, 2006; Kyriazakis and Sandberg, 2006; Luiting and Knap, 2006; van Milgen et al., 2012). Whittemore and Fawcett (1974, 1976) proposed one of the first nutritional models describing pig growth, with the objective of predicting body protein and lipid deposition from the energy and protein intake. The basic concepts underlying this semi-mechanistic model can be summarized as follows (van Milgen et al., 2012):

- Growth is determined from modelling lipid and protein deposition; BW,
 water, and ash deposition, and fat and lean weight are calculated empirically
 from body protein and lipid weight
- The model considers an upper limit to protein deposition in growing pigs, which is constant during growth (i.e. PDmax, 110 g/day from 20 to 100 kg)
- There is a minimum lipid-to-protein deposition ratio (minimum LD:PD)
- The actual protein deposition is determined by the last two factors and by the quality and quantity of ingested protein (i.e. the supply in essential amino acids)

 Feed intake is a model input; energy not used for maintenance or protein deposition is used for lipid deposition that is therefore considered as an energy sink.

An important concept used in this model was the linear–plateau relationship between ingested energy and protein deposition, with protein deposition being dependent on (linear part, minimum LD:PD) or independent of (plateau or PDmax) the energy supply.

The concepts of Whittemore and Fawcett (1974, 1976) have been used and developed further in several models such as those of Black et al. (1986), Moughan et al. (1987), Pomar et al. (1991a), Ferguson et al. (1994), de Lange (1995), Emmans (1997), Wellock et al. (2003), van Milgen et al. (2008), Yoosuk et al. (2011), NRC (2012) and Strathe et al. (2015). These models are often based on the nutrient partitioning concepts of Whittemore and Fawcett (1974, 1976), which are summarized by de Lange (1995) and van Milgen et al. (2012). Ingested nutrients are partitioned between maintenance requirements (including also endogenous losses and a minimum protein turnover rate) and requirements for protein and lipid deposition and their corresponding efficiencies. Body weight and carcass traits are determined from these depositions. Compared to the approach of Whittemore and Fawcett, various modifications have been proposed, for instance concerning the change in PDmax and the relationship between ingested energy and protein deposition during growth (van Milgen et al., 2008; NRC, 2012). In these models, feed intake can be considered as an input ('push' approach) or an output ('pull' approach). In the 'push' approach, ad libitum feed intake is typically modelled as a function of BW through linear, exponential, power, or gamma functions (e.g., Moughan et al., 1987; Pomar et al., 1991a; de Lange, 1995; van Milgen et al., 2008; NRC, 2012). Because lipid deposition is considered as an energy sink, energy not used for maintenance and protein deposition is deposited as lipid. Unless a specific control of energy intake is included in the model (e.g. with the Gamma function where animals eat for maintenance when they approach maturity), there will be no constraint on the way lipid deposition will evolve during growth. In the models of Black et al. (1986), Ferguson et al. (1994), Emmans (1997), Wellock et al. (2003) and Yoosuk et al. (2011), a 'pull' approach was used where feed intake is calculated to satisfy the requirements of maintenance and of the potential protein and lipid deposition. In these models, explicit response curves (e.g. Gompertz functions) are used to describe the change in the

potential protein and lipid deposition during growth. Actual intake is then calculated from predicted feed intake by applying constraints such as ingestion capacity of animal, feed characteristics (e.g. nutrient composition, density and water holding capacity) or environmental conditions (e.g. temperature). In this approach, when the animal tends to maturity, protein and lipid deposition tends towards zero and feed intake corresponds to the energy expenditure for maintenance.

The different models presented here predict growth, as affected by nutrient supply, animal characteristics and, in some cases, housing conditions. These models allow one to calculate nutrient requirements to achieve this growth and identify possible limiting factors. Most of these models depend on a large number of parameters that are difficult to obtain or estimate under practical conditions. Although these models are used in a research context, practical application of models requires that these models are easily accessible and user-friendly (e.g. as a dedicated software tool) and that required model inputs can be provided by the user (e.g. TMV (Werkgroep 1991), NRC (2012) and InraPorc (Dourmad et al., 2008; van Milgen et al., 2008)). For example, the InraPorc software summarizes the phenotypic potential of a growing pig (i.e. growth potential and *ad libitum* feed intake) by five model parameters. These parameters can be estimated through a statistical routine using on-farm recorded data of body weight and feed intake. Tools such as InraPorc can be used to estimate nutrient and energy requirements and utilization, evaluate the consequence of different feeding strategies, and identify feeding strategies that allow one to improve performance traits such as feed efficiency. An example of the change in nutrient and energy utilization during growth obtained from InraPorc is given in Fig. 1 for the utilization of digestible energy (Fig. 1a) and standardized ileal digestible (SID) lysine (Fig. 1b) as a function of BW. Van Milgen et al. (2009) illustrated the use of InraPorc to adapt feeding strategies and they simulated the performance of a pig between 27 and 100 kg BW having an average daily feed intake of 2.74 kg/d and an average daily gain (ADG) of 1.10 kg/d. Diets were formulated on a least-cost basis using feed ingredient prices of May 2008 in France and a net energy content of 10 MJ/kg. A first diet (D1) was formulated to contain 9.2 g SID lysine, a level 10% higher than the requirement of the animal at the start of the studied period to account for the requirement of the population (see Section 3.1). Two others diets (D2 and D3) were formulated with lower SID lysine levels corresponding to the requirement

at around 60 kg BW and at the end of the studied period. Three feeding strategies were then defined: a single phase strategy with D1 (SP), a two-phase strategy with D1 offered until 60 kg BW and D2 for higher body weights (TP), and a multiphase strategy (MP) with a progressive replacement of D1 by D3 to follow as much as possible the changes in the SID lysine requirement. Growth performance obtained for the three strategies were identical as the diets were formulated to avoid deficiencies. However, total nitrogen (N) intake decreased from 4.79 kg for SP to 3.86 kg for MP. Consequently, N excretion decreased from 3.01 kg for SP to 2.08 for MP, and the efficiency of N utilization was increased. In addition, better adapting the nutrient supply to the requirement reduced feed costs (in comparison with the SP strategy) by 5.4% for TP and by 10.8% for MP. This example shows the interest of using modelling nutrient requirements to improve feed efficiency.

FIGURE 1 TO BE PLACED HERE

Figure 1. Simulation of changes in digestible energy (a) and lysine requirements (b) depending on body weight, for animals with an average daily gain of 763 g/d and a feed to gain ratio of 2.95 kg/kg

2.2 Models for reproducing sows

In contrast to models for growing pigs, only few models describing nutrient utilization in reproductive sows have been developed (Williams et al., 1985; Dourmad, 1987; Pomar et al., 1991b; Pettigrew et al., 1992; Dourmad et al., 2008; NRC, 2012; Hansen et al., 2014), and most of these are research models. Some of these are more of calculation models to determine nutrient requirements (e.g. NRC 2012). More mechanistic models also exist, such as InraPorc (Dourmad et al., 2008) and Hansen et al. (2014). These two models describe energy and nutrient partitioning on a daily basis using a similar structure. The calculation of nutrient requirements during gestation and lactation, that are differentiated, is based on a factorial approach. As for growing pigs, the sow models are based on body lipid and protein mass that evolve as a function of the flows of (metabolizable) energy and digestible amino acids. During gestation, requirements for maintenance (including activity and thermoregulation) and foetal/uterus and maternal

growth are modelled. During lactation, nutrient and energy requirements are based on the requirements for maintenance, milk production and maternal growth. Priority of nutrient use is given to maintenance, foetal growth and milk production. Body reserves can be mobilized to contribute to these functions in case the nutrient supply is lower than the requirement during lactation. Conversely, body reserves can be (re)constituted during the next gestation when the nutrient supply exceeds the requirements for maintenance and foetal growth.

Compared to other models, the InraPorc sow model allows calibrating parameters from on-farm data of reproductive performance, feeding practices and housing conditions. These parameters can be used to calculate nutrient requirements by the factorial approach, and to simulate the dynamic response of sows to different feeding strategies. An example of the SID lysine utilization by sows over four parities is given in Fig. 2 (Dourmad et al., 2015a). Three different feeding strategies were used that differed in nutrient supplies during gestation. With the first feeding strategy (Fig. 2a) a single gestation diet was used during the entire gestation period and a lactation diet during lactation. The feeding level during gestation increased by 400 g/d during the last 3 weeks of gestation and was adjusted to body condition at mating and the target body condition at farrowing. During lactation, feed intake was assumed to be close to ad libitum. Diets were formulated on a least-cost basis. The Fig. 2a indicates that the SID lysine requirement increases during gestation but decreases with parity (because the sows attain mature BW). Consequently, for gestating sows receiving the same diet independently of parity, the amino acid and protein supplies exceed the requirement, especially during the beginning of gestation and more so in older sows. To test the possibility of reducing this excess, a second strategy was simulated using two different diets for gestating sows, depending on parity and gestation stage, and differing in amino acid and protein contents (Fig. 2b). The first diet contained 3.8 g SID lysine and 102 g crude protein (CP) per kg of feed and was used during the first 80 days of gestation, except for first parity sows. The second diet contained 5.5 g SID lysine and 145 g CP per kg of feed and was used in first parity sows throughout gestation, and in other sows from day 80 of gestation. Other amino acids were supplied according to the ideal protein requirement. With the two-phase strategy, total consumption of CP and SID lysine were reduced by 10 and 11%, respectively, with an associated average reduction of 15% of N

excretion. These results indicate that the amino acid supplies were much better adjusted to the sow's requirements with this strategy. Further improvements have been tested using a multiphase feeding during gestation. Two gestation diets were formulated differing in amino acid and CP contents. The first and the second diets contained 3.0 g SID lysine and 99.7 g CP, and 5.5 g SID lysine and 145 g CP per kg of feed, respectively. The two diets were mixed in adequate proportions to meet, on a daily basis, the amino acid (and digestible P) requirement (Fig. 2c). Compared to the single diet feeding strategy, intake of CP and SID lysine and N excretion were reduced by 14, 17 and 2% respectively, with the multiphase strategy. Compared with the one-phase feeding strategy (and without considering the possible extra cost for applying the feed changes), the calculated feed cost was 6% lower with the two-phase strategy, and 8% lower with multiphase feeding. Modelling nutrient requirements can thus be used to develop feeding strategies to improve feed efficiency and to reduce N excretion and feed costs.

FIGURE 2 TO BE PLACED HERE

Figure 2. Simulated effect of different gestation feeding strategies on the utilization of ileal digestible lysine (a): one diet, (b): two diets in multiparous sows with a change at day 80 of gestation, (c): two diets mixed in adequate proportions to meet lysine and apparent digestible phosphorus requirements from Dourmad et al., (2015a).

2.3 Mineral requirement modelling

As described above, many current growth models for pigs consider that BW, water and ash deposition, and fat and lean weight are determined from body protein and lipid weight, as suggested by Whittemore and Fawcett (1976). Van Milgen et al. (2008) and NRC (2012) estimate empty BW and BW from protein and lipid body mass without explicitly determining water and ash mass. As indicated by Létourneau-Montminy et al. (2015), these approaches imply that body ash (i.e. all body minerals) mass and growth are driven by growth of body protein and/or lipid. Létourneau-Montminy et al. (2015) observed that pigs fed deficient diets modulated growth of soft tissues and bone mineralization independently (Pomar et al., 2006; Rousseau, 2013). Consequently, total body ash can be reduced without necessarily reducing mineral deposition and growth of soft tissues. Minerals are of great importance in pig nutrition. For instance, phosphorus (P) has an important role in bone development and metabolism of growing pigs (NRC 2012). It also has an important economic value, being the third most expensive nutrient in pig diets after energy and protein. Indeed, due to the low digestibility of dietary P of plant origin (i.e. phytate), diets are supplemented with expensive, non-renewable inorganic sources of P to meet the P requirements (Selle et al., 2011). The alternative, often used in practice, is to incorporate phytase enzymes which increase P digestibility. The high excretion of P, due to its oversupply and its low digestibility, also contributes to the environmental impact of pig production through eutrophication (Selle et al., 2011). These different elements argue to use precise modelling approaches to determine mineral requirements in order to be able to achieve an optimized supply, with minimized excretion.

The factorial approach of mineral requirements has been integrated in models for growing pigs and sows. For instance, Jondreville and Dourmad (2005) estimated P requirements for maintenance and production for different physiological stages. These principles have been integrated in models such as InraPorc for growing pigs (van Milgen et al., 2008) and sows (Dourmad et al., 2008) using the concept of apparently digestible P and considering the effect of diet form (pellet or mash) and phytase addition on digestibility. As summarized by Noblet et al. (2016), the P requirement for growth is based on the BW of animals. Export of P through milk is estimated from milk protein production while P requirement for conceptus growth is estimated from protein deposition in foetuses. The approach proposed by Jondreville and Dourmad (2005) allows one to adjust the dietary digestible P supply to pig performance and physiological status, and to evaluate the effect of performance level on apparent digestible P requirement. For instance, a decrease of 0.2 points in feed conversion ratio in growing pig requires an increase of 0.2 g/kg in dietary P concentration.

As indicated earlier, estimating mineral requirements from performance (i.e. BW or BW gain) has some limitations. Consequently, specific models have been developed, mainly for P, to allow the body mineral content to vary independently of protein and lipid mass and to allow simulating different phases of P deficiency (e.g. a phase of bone weakening while performance is maintained followed by a phase of growth reduction) and compensatory bone mineralization (Fernandez, 1995; Schulin-Zeuthen et al., 2005; Létourneau-Montminy et al., 2007, 2011, 2015; Symeou et al., 2014a,b). These models

are deterministic and mechanistic as they explicitly consider the mechanisms of P intake, digestion, retention and excretion (e.g. Symeou et al., 2014a,b), and also of Ca and other minerals and natural or microbial phytase addition (e.g. Létourneau-Montminy et al., 2015). Steps of mineral digestion in the stomach, and in the small and large intestine, can be differentiated (e.g. Symeou et al., 2014a,b) as well as excretion in the urine and faeces. These models are mainly oriented towards research but are aimed to be included in decision support tools and can be applied to develop feeding strategies in relation to growth performance, bone mineralization and optimization of P retention while minimizing P excretion.

3 Population, variability and feed requirement modelling

3.1 Interest to include variability in pig models

As described above, several models exist to determine nutritional requirements. However, these models are mainly deterministic, representative for average animal. Furthermore, parameter values used in these models are obtained from experiments conducted with groups of pigs, for which the average animal is supposed to be representative (Pomar et al., 2013). Different arguments can be advanced in favour of considering not only the average animal but also the variability among animals. Knap (1995) pointed out some arguments for considering variability in models. For example, the profitability of production systems can be largely affected by the extent of variability of performance traits. Moreover, the change from a production system to another can have minor effects on mean production levels but important consequences on their variability. For example, offering feed *ad libitum* in the finishing period can have limited impacts on the population mean of ADG in comparison with a restricted feed allowance. However, it can induce an increase in the variability in ADG among animals, influencing the BW and lean content distribution at slaughter and thus impact carcass payment. Additionally, when using a model for replacing experimental comparisons by simulations, the inclusion of variability in models is needed as a proper significance testing of differences between production systems requires statistical tests based on knowledge of variability within and between systems. Indeed, a difference between

treatment means is meaningful only if it can be compared to the variation within each treatment. A last example is the study of the relationships between performance criteria, for which covariance between these criteria and thus variability must be accounted for. Recent studies have demonstrated the importance of considering variability among animals to evaluate biological responses and in defining nutritional programmes (Pomar et al., 2003; Main et al., 2008; Brossard et al., 2009; Vautier et al., 2013). Indeed, between-animal variation determines the population response and, therefore, the overall efficiency of nutrient utilization (Pomar et al., 2003) and optimal nutrient levels (Leclercq and Beaumont, 2000; Pomar et al., 2003; Brossard et al., 2009). Pomar et al. (2003) and Pomar (2005) illustrated this point by using a growth model based on those of Knap (1999) and Wellock et al. (2003). The inputs of the model are the diet composition and the pig genotype, which is described by three independent parameters. This model was used to simulate the growth of 2500 pigs originating from five different populations with the same mean genetic potential (i.e. the same mean values for each of the three model parameters) but with different genetic variances. Populations were generated randomly to obtain for each parameter 0, 0.5, 1, 1.5 and 2 times the estimated genetic variance from a reference population. Consequently, the null variance population corresponded to a population of fully identical animals, while other populations corresponded to more or less heterogeneous populations. The performance of pigs was simulated during one day considering that all pigs were 50 kg BW. Simulations were carried out with 11 diets, with intake of ideal protein varying from 212 to 290 g/d. For the null variance population, the response of protein deposition to increasing protein supply had a linear-plateau shape, as stated in the single animal model (Fig. 3a). With an increasing variance of parameters, the response became increasingly curvilinear-plateau and the protein level required to attain the plateau increased as the variance increased. The ideal protein requirement, defined as the nutrient level required to maximize protein deposition, increased from 235 g/d to 251 g/d when the variance increased from 0 to 1 times the reference variance. For higher variance, the requirement value was difficult to estimate because some animals in the population did not receive sufficient protein to express their potential (Fig. 3b). The average animal is represented by the null variance population for which the requirement is met for a supply of 235 g/d. For other populations, this supply allowed covering the requirements of 50% of the population. This percentage of pigs with their

requirement met was decreased when the protein supply was reduced, the extent of this decrease being higher when the population variance increased. Similarly, the proportion of over-fed pigs increased when the protein supply increased. In the same way, Brossard et al. (2009) also showed that the SID lysine requirement varies between pigs in a population and that the percentage of pigs for which the requirement was met can vary greatly with the feeding strategy (e.g. then number of feeding phases) and the growth period.

FIGURE 3 TO BE PLACED HERE

Figure 3. Effect of growth parameters variability between individual pigs (0, 0.5, 1, 1.5 and 2 times the variance of a reference population) and quantity of ingested protein on daily protein deposition (a) and percentage of under-fed pigs (b) for 50 kg BW pig population from Pomar et al. (2005).

3.2 Integrating variability in feed requirement modelling

To account for the variability among pigs in determining nutrient requirements and to study the effect of feeding strategies on performance, different models have been developed to simulate the growth of a pig population (e.g. Ferguson et al., 1997; Knap, 1999; Pomar et al., 2003; Wellock et al., 2004; Brossard et al., 2009; Symeou et al., 2016a,b). These approaches are based on the knowledge of mean values and variability (mainly through variance, rarely through covariance) of model parameters. Different methods can be used to estimate these values. Schinckel and de Lange (1996) proposed repeated measurements of body composition using ultrasounds or tomography to assess individual variability during growth. Methods of inversed modelling have also been developed to obtain these parameter values for a population or for individual animals (Knap et al., 2003; Doeschl-Wilson et al., 2006; Vautier et al., 2013). For instance, model parameters can be adjusted iteratively through optimization by comparing real data (e.g. BW, feed intake, protein or lipid mass) to model outputs to minimize the difference between predicted and real values.

Once the mean and the variance of parameter values are known, different methods can be applied to integrate variability in models. For instance, combinations of a limited

number of parameters can be generated randomly from mean and variance values of parameters. Parameters are supposed to have normal and independent distributions and the coefficient of variation (CV) of parameters are fixed by authors. The lack of information constrained the authors to ignore the covariance between parameters (e.g. Ferguson et al., 1997; Pomar et al., 2003; Wellock et al., 2004; Symeou et al., 2016a,b). Indeed, Ferguson et al. (1997) considered it too costly and difficult to develop experimental procedures to obtain a correct estimation of CV and correlations between parameters. However, not considering covariance between parameters induces an overestimation of simulated variability (Pomar et al., 2003). For example, a parameter describing feed intake is undoubtedly correlated to a parameter describing growth because a pig eating more than average is also likely to grow faster than the average pig. Therefore, introducing variability in models requires knowledge not only of the variance in parameter values but also of the covariance between parameters (Ferguson et al., 1997; Kyriazakis, 1999). Consequently, other methods have been developed to integrate covariance between parameters. Morel et al. (2010, 2012) used a model in which the pig genotype is described by three parameters. Combining a correlation matrix between parameters obtained from literature and different levels of CV, they calculated a variance-covariance matrix, and thus generated different populations using this variance-covariance matrix and different mean values. Brossard et al. (2009, 2010) and Vautier et al. (2013) obtained a variance–covariance matrix for the five parameters describing the growth potential and feed intake of the InraPorc model through inversed modelling. Brossard et al. (2009) determined parameter values for 192 pigs, allowing one to study correlations between parameters and to obtain mean values and a variance-covariance matrix of the parameters. These last two elements allow the generation of virtual populations of pigs with the same characteristics as the initial population in terms of mean values and variability. For the same model parameters, Vautier et al. (2013) developed a methodology for the generation of pigs populations based on a generic variance-covariance matrix associated with distribution laws of the parameters. The generic variance–covariance matrix was calculated as a median from matrices obtained from 40 subpopulations of pigs differing in sex and cross-breeds, to ensure the genericity of the relationships between parameters and to avoid the use of a particular variance-covariance structure. This generic matrix and the distribution laws can be combined with mean parameters obtained on-farm to generate virtual

populations of pigs with realistic mean performance and variability. Finally, Schinckel et al. (2003) and Strathe et al. (2009, 2010) developed stochastic growth models using nonlinear mixed equations, integrating a mean effect of the population and random effects due to individuals. Their method allows one to obtain a mean value for each parameter but also individual values and correlation and variance–covariance structures that can be used to generate populations and perform stochastic simulations and predictions of mean and standard deviation of performance.

3.3 Applying stochastic modelling to feed efficiency improvement

The stochastic growth models presented above can be used to simulate the effect of different feeding strategies on animal performance but also on economic results and environmental impacts. Morel et al. (2010, 2012) applied their model to investigate how pig genotype (i.e. lean, normal and fat), population size and variability, feed costs, carcass payment scheme, and feed allowance (i.e. restraint vs ad libitum) affect the gross margin and/or N retention that are optimized through feeding strategies (i.e. number of diets, energy and amino acid content, quantity and duration during which each diet is fed). Morel et al. (2010) randomly generated populations of 1 to 625 pigs by varying four parameters of a growth model. Variation of these parameters around the mean was modelled by a CV of 0% (single pig population), 5, 10 or 20%. To generate populations, the parameters were considered either independent or correlated with an associated covariance matrix for the parameters, as described in Section 3.2. Populations were generated for lean, normal or fat pig genotypes. Diets used changed each week; levels of digestible energy (DE) and ratio digestible lysine (Lysd)/DE used for formulation of diets were determined by nonlinear optimization with a genetic algorithm on the basis of simulated performance between 20 and 85 kg BW with an objective of maximizing gross margin (i.e. carcass value minus feed costs and piglet value). Their results showed that lean pigs allowed one to obtain the highest gross margins. The variability in gross margin between simulation runs increased with increasing population variability but decreased with increasing population size. When the covariance was introduced, difference in optimal Lysd/DE ratio varied from -4% to 50% between single pig population (average pig) and population of 125 pigs, depending on the pig type. These authors also noticed that including variance increased optimal values for Lysd/DE ratio.

In conclusion, this study showed the importance of the knowledge and the inclusion of variability in the optimization of gross margin through adapted feeding strategies. Brossard et al. (2010) used a stochastic model for an economic and environmental analysis of pig production. They simulated the effect of changing the SID Lys/net energy (NE) ratio from 85 to 115% of the average population requirement on growth performance, economic results, and N excretion in two contexts of costs of feed ingredients (high or moderate). These different Lys/NE ratios were combined with three different feeding strategies: one strategy with a single diet formulated to meet the mean requirement at the beginning of the growth period; a two-phase strategy with a grower diet and a finisher diet formulated to meet the mean requirement at the beginning and at the middle of growth period; a multiphase strategy with daily adjustments of the diet to the mean requirement of the population. Performance and N excretion were simulated from 27 to 112 kg BW with InraPorc®. Gross margin was calculated from carcass value and feed and labour costs. Maximal growth performance was observed with a SID Lys/NE ratio of 105 to 115% of the mean requirement (Table 1) illustrating the fact that the nutrient supply required to maximize growth performance is higher than mean population requirement. Reducing the SID Lys/NE ratio below 100% of the mean requirement reduced growth performance and economic results, with the effect being more marked for the two-phase and multiphase strategy. It also increased N excretion for the multiphase strategy but decreased N excretion for the single diet strategy. Indeed, the daily adjustment of SID Lys supply below the mean requirement implied that a major part of the population encountered a SID Lys deficiency, consequently reducing the N efficiency. In contrast, with the single diet strategy, reducing SID Lys supply reduced the SID Lys oversupply and thus the N excretion. When the SID Lys/NE ratio in diets was increased above 100% of the mean requirement, economic result was improved for two-phase and multiphase strategy with an optimum with a SID Lys/NE ratio of 110 to 115% depending on cost context and strategy. For the multiphase strategy, this economic improvement was accompanied by a small reduction in N excretion, whereas the two other strategies induced higher N excretion. For growing-finishing pigs, Niemi et al. (2010) used a bio-economic stochastic dynamic programming model with a growth component and an optimization of the timing of slaughter and daily amounts of protein and energy used in the feeds. Their results suggested that a switch from the classical two-phase feeding to a multiphase

feeding adjusting daily the supplies can increase the annual return by 1.35–1.88 € per pig place. For sows, as illustrated above with the results of Dourmad et al. (2015a) (Fig. 2), application of multiphase feeding could also improve feed efficiency and could reduce N excretion up to 19%. More recently, Monteiro et al. (2016) used a similar approach combined with life cycle assessment to evaluate the interest of different formulation and feeding strategies for reducing the environmental impact of pig fattening in France and Brazil. These different examples illustrate that modelling approaches accounting for individual variability are very helpful in identifying feeding strategies that allow one to improve feed efficiency and gross margin and that can contribute in reducing the environmental impact.

TABLE 1 TO BE PLACED HERE

Table 1. Effect of feeding strategy¹ and dietary digestible lysine to net energy ratio on feed conversion ratio, gross margin² and nitrogen excretion, for a virtual population of 1000 pigs from Brossard et al. (2010).

Paramete	Feeding	Dietary Lys/NE content (% of reference level)						
r	strategy	85	90	95	100	105	110	115
F:G (g/g)	1-phase	2.75	2.70	2.67	2.66	2.66	2.65	2.65
	2-phase	2.88	2.79	2.72	2.69	2.67	2.66	2.65
	Multiphas							
	е	3.09	2.94	2.83	2.75	2.70	2.67	2.66
Gross margin	1-phase	-3.8	-1.8	-0.6	0.0	0.1	0.0	-0.4
	2-phase	-9.8	-5.7	-2.7	-1.1	-0.2	0.2	0.2
(∆€/pig)	Multiphas	-18.	-12.					
	e	7	7	-7.7	-4.0	-1.8	-0.5	0.0
Nitrogen excretion (kg/pig)	1-phase	3.14	3.27	3.44	3.61	3.84	3.88	3.88
	2-phase	3.23	3.15	3.10	3.24	3.39	3.53	3.59
	Multiphas e	3.66	3.47	3.34	3.27	3.26	3.24	3.27

¹1-phase strategy: single diet containing 9.71 MJ net energy (NE)/kg and 0.762 g SID Lys/MJ NE for the 100% reference level; 2-phase strategy: two successive diets (9.71 MJ NE), with a diet change at 112 days of age, and containing 0.762 g SID Lys/MJ NE and 0.635 g SID Lys/MJ NE, respectively, for the 100% reference level; multiphase strategy: the Lys/NE ratio was changed daily according to requirements, with an NE supply of 9.71 MJ and a SID Lys supply for the 100% reference level of 0.762 g/MJ NE and 0.531 g/MJ NE at the beginning and at the end of the growing-finishing period, respectively. ²Difference relative to the 100% Lys/NE level of the 1-phase strategy.

4 Towards precision feeding

As indicated above, modelling approaches exist that deal with variability in requirements among individual pigs. This allows one to define how to feed a population, on a basis of a reference (e.g. mean animal) and of simulations on populations generated using the knowledge of mean or individual values of parameters and/or variance–covariance relationships between parameters. Even if these approaches are useful to explore optimal feeding strategies, some difficulties can arise when considering these approaches. Depending on the approach followed, obtaining appropriate parameters or variance–covariance knowledge for a given population can be difficult. Moreover, parameters obtained for one population cannot be adapted for another population due to differences in parameter variability or housing conditions.

To account for variability among pigs without dealing with issues such as covariance structure between parameters, a new approach for nutrient requirement modelling is offered by precision feeding, concomitantly with the development of technologies in the field of precision farming. Precision feeding is based on the dynamic adjustment (if possible day by day) of dietary nutrient supplies to requirements, at a group or at an individual level. In this approach, individual pigs are treated as such and each pig/group is to be modelled individually. The purpose is to improve feed efficiency whilst reducing feed cost and environmental impact. To provide daily and individual tailored diets, this technique needs to include the following elements (Pomar et al., 2009, 2013):

- the precise evaluation of the nutritional value of feed ingredients,

- the real-time determination of nutrient requirements of individual pigs,

- the formulation of balanced diets limiting the amount of excess nutrients, and

- the concomitant adjustment of the dietary supply of nutrients that will match the estimated requirements of the individual pig.

Real-time data collection is needed in terms of BW and feed intake through automatic devices. To obtain model parameters by individual and to predict nutrient requirements and performance individually and on a daily basis using real-time data, models have to evolve to integrate 'real' growth and feed intake patterns that may differ from the expected 'theoretical' patterns. Hauschild et al. (2010a, 2012) developed a prediction model combining a statistical real-time estimation of expected BW gain and feed intake (depending on realized performance during the preceding days) with a mechanistic model predicting protein deposition and NE intake and calculating by the factorial method the amino acid and mineral requirements to sustain this performance. Knowing the requirements for a pen or an individual pig, an optimal blend of feeds can be defined and distributed to individual pigs. Pomar et al. (2010) used this model to simulate the effect of applying precision feeding at an individual level. Their results indicated that precision feeding, by daily and individual adjustment of nutrient supplies to requirements, reduced feed cost by 11% and N and P excretion by more than 38%, compared to three-phase feeding applied to the whole group. This study indicates the potential of precision feeding in improving feed efficiency. The application of precision feeding using real-time modelling of nutrient requirements was tested for growingfinishing pigs over an 84-day fattening period. Pigs received a classical three-phase feeding programme (3P) obtained by blending fixed proportions of feeds A (high nutrient density) and B (low nutrient density), or a daily-phase feeding programme in which the blended proportions of diets A and B were adjusted daily to meet the estimated nutritional requirements of each individual pig (multiphase individual feeding, MPI). The performance (ADG, average daily feed intake, gain to feed ratio and N and P retention) obtained with the MPI programme were similar to those obtained for the 3P programme. However, compared with the 3P programme, the application of MPI programme reduced the SID Lys intake by 27%, the estimated N excretion by 22%, and the estimated phosphorus excretion by 27% (Table 2; Andretta et al., 2014). In Andretta et al. (2016), the application of MPI programme reduced SID lysine intake, estimated N excretion and feeding costs by 26, 30 and 10%, respectively. Even if the reduction in excretion and feed costs is smaller than this estimated by simulation, these results confirm the possibility of improving feed efficiency (for instance in terms of feed cost and environmental impact) with the combination of real-time modelling of requirement with precision feeding. This approach has yet to be improved for a further application

on-farm, to be able to integrate more information on animal (e.g. composition of BW gain, health status and behaviour) and its environment (e.g. temperature and ventilation rate) that are made available by the development of sensors, and that can modulate accuracy of predictions. Additionally, more complex objectives for feeding strategies could be integrated such as body composition, expected weight at fixed age to plan slaughter departures, and so on.

TABLE 2 TO BE PLACED HERE

Table 2. Performance, digestible lysine intake and nitrogen and phosphorus excretion for pigs fed during 84 days with three successive diets applied for the whole group (Group) or by individual precision feeding (Precision) from Andretta et al. (2014)

	Feeding strategy			
Parameters	Group	Precision		
Initial weight (kg)	40.1	42.7		
Final weight (kg)	133.8	135.8		
Daily feed intake (kg/d)	3.05	3.05		
Ingested digestible Lysine (g/d)	23.8ª	17.4 ^b		
Average daily gain (kg/d)	1.11	1.10		
Feed conversion ratio (kg/kg)	2.63	2.70		
Nitrogen excretion (g/d)	48.1ª	37.7 ^b		
Phosphorus excretion (g/d)	6.9ª	5.1 ^b		

Different subscripts within a row indicate statistical difference (P < 0.05).

5 Case study

Using modelling approaches to determine feed requirements and to adapt feeding strategies has been shown by simulation to improve feed efficiency (see Section 3.3). Some studies have also been developed to assess the practical application of these

modelling approaches. For instance, Brossard et al. (2014) used a herd modelling approach to evaluate different feeding strategies to control or reduce variability among pigs at slaughter. Indeed, the variability in BW among animals complicates the management of slaughter departures. These departures are planned to deliver each time a sufficient number of animals within BW range allowing a maximal payment of carcass. Controlling the variability of BW at slaughter is thus important to be able to deliver a maximal number of animals in the targeted BW range and to avoid too light or too heavy pigs. The applicability and accuracy of this approach was assessed in an experimental study using some of the feeding strategies evaluated by simulation. The InraPorc model was used to perform simulations on 10 batches, each of 84 cross-bred pigs (half barrows and half gilts), to characterize the effect of feeding strategies differing in the amino acid supply or feed allowance, on the mean and variation in growth rate and slaughter weight. In the simulations concerning feed allowance effect, pigs were offered feed *ad libitum* or were restricted (increase in feed allowance by 27 g/day up to a maximum of 2.4 and 2.7 kg/day for gilts and barrows, respectively). A two-phase feeding strategy was applied to all animals, with 0.9 and 0.7 g of digestible lysine per MJ of net energy (NE) in diets provided before or after 65 kg BW, respectively. Pigs were supposed to be slaughtered in two departures, with a mean BW at departure of 112 kg for the whole population. Results indicated that a feed restriction reduces the CV of BW at first departure for slaughter (BW1) and at slaughter by 34% (from 9.0 to 5.9%) and 26% (form 7.9 to 5.8%), respectively. Growth performance obtained from in silico simulations using *ad libitum* and restricted feeding plans was compared with results obtained in an in vivo experiment on a batch of 168 pigs when applying exactly the same feeding and slaughtering strategies. Actual growth was similar to that obtained by simulation. The CV of BW1 was also similar in vivo and in silico for the *ad libitum* feeding strategy but was slightly underestimated by 1 percentage point in silico for the restriction strategy. This study confirms the relevance of using simulations to predict the level and variability in performance of group-housed pigs, and the possibility of control of variability through feeding strategies.

A precise knowledge of nutrient requirements in growing pigs and reproductive sows is required to better adapt feeding strategies and thus increase feed efficiency and economic results, and reduce the environmental impact of pig production. Modelling approaches have been developed to integrate this knowledge and allow taking into account the possible interactions between the pig and production conditions. Recent development to integrate the effect of individual variability on requirement estimations allowed better accounting for these interactions. Even though additional research is still required, modelling approaches appear to be interesting alternatives and complements to experimentation. Modelling nutrient requirements is a powerful tool to test the effect of different feeding strategies on a set of criteria of interest (e.g. efficiency of nutrient utilization (and thus environmental impact), economic results). Testing a large set of feeding strategies by actual experiments would be too expensive and complicated in field situations. Moreover, results of virtual experiments give indications or trends for future improvements in feeding practices depending on farm situation and animal potential. Research models can be included in decision support tools for technicians and farmers and can also be directly integrated into automatized systems such as precision feeding systems. However, and even if current models already allow good predictions of animals requirements performance, further developments are still in progress for their improvement.

Current nutritional models allow defining nutrient requirements depending on pig characteristics. Some pig models for growing pigs are now including variability among animals in terms of growth and intake potentials. Also models for sows can account for variability among animals and within a given animal depending on parity or gestation/lactation stage. Future research for these models is aimed to integrate other sources of variation. For sows, the effect of ambient temperature, activity, parity or litter size on requirements are still to be refined and integrated more properly in models (Ngo et al., 2012; Dourmad et al., 2015b). In the same way, growing pig models have to be refined to better integrate the effect of ambient temperature (Wellock et al., 2003; Renaudeau et al., 2011), animal activity or capacity to deal with different stress sources linked to their social environment (e.g. group size, surface per animal, mixing period, as in the model proposed by Wellock et al., 2004) or health status. The effect of health status on resource allocation and the associated mechanisms have to be investigated to be integrated in models. Concerning minerals, comprehensive models were made available recently (e.g. Létourneau-Montminy et al., 2015) but refinements are still required to better account for changes in body mineral reserves and the mechanisms involved in the regulation of absorption. This will allow accounting for resorptionabsorption phases in sows or compensation between phases in fattening pigs. Availability of sufficient and adapted data is required to support these developments and their application for improving feed/nutrient efficiency. The current development on sensors and data collection to characterize pigs at an individual level or on their environment will allow the access in real time and with a higher frequency to more precise data on classical characteristics (e.g. feed intake, BW and ambient temperature) but also to other new traits such as behaviour, body composition and health status. The prediction of nutrient requirements will then be supported by models integrating these different types and sources of data, on the basis of historical data and also in real time. It can be imagined that the requirements will be defined not only for simple production objectives (e.g. feed intake and growth) but also for multicriteria objectives such as economical return and environmental impact.

7 Where to look for further information

- A good introduction to the subject for non-specialists is provided by the article of Noblet et al. (2016, see reference above)

Some books exist on feed efficiency and modelling: 'Mechanistic modelling in pig and poultry production' (2006, Eds R. Gous, T. Morris and C. Fisher, CABI Publishing, Wallingford, UK); 'Mathematical modelling in animal nutrition' (2008, Eds J. France and E. Kebreab, CABI Publishing, Wallingford, UK); 'Feed Efficiency in Swine' (2012, Ed J. F. Patience, Wageningen Academic Publishers, Wageningen, The Netherlands); 'Nutritional modelling for pigs and poultry' (2015, Eds N. K. Sakomura, R. M. Gous, I. Kyriazakis and L. Hauschild, Cabi Publication, Wallingford, UK).

- Every year, the European Federation of Animal Science (EAAP, www.eaap.org) organizes its annual meeting with sessions on pigs with a focus on feed use or feed

efficiency, and also since 2016, a dedicated commission for PLF (precision livestock farming). Every five years, the international Workshop 'Modelling Nutrient Digestion and Utilization in Farm Animals' (Modnut) is organized (see http://www.jackiekyte.com.au/modnut2014/for the last one).

- The EU H2020 Feed-a-Gene project (www.feed-a-gene.eu/) aims to better adapt different components of monogastric livestock production systems (i.e. pigs, poultry and rabbits) to improve the overall efficiency and sustainability. This includes the modelling of biological functions with an emphasis on feed use mechanisms to better understand mechanisms of feed efficiency.

- A list of research centres readers can investigate, for example, for possible collaboration as well as to keep up with research trends:

- French National Institute for Agricultural Research (INRA) (www.inra.fr/)
- Agriculture and Agri-Food Canada (AAC) (www.agr.gc.ca/)
- Wageningen University and Research (WUR) (https://www.wur.nl/)
- Newcastle University (www.ncl.ac.uk/)

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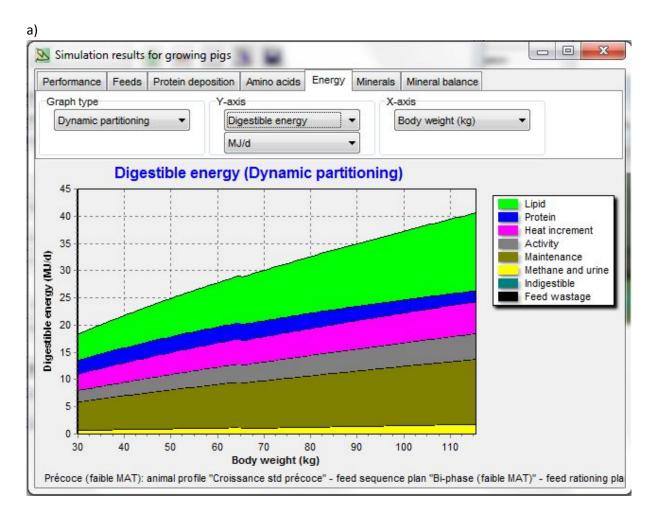
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Figure 1. Simulation of changes in digestible energy (a) and lysine requirements (b) depending on body weight for animals with an average daily gain of 763 g/d and a feed to gain ratio of 2.95 kg/kg



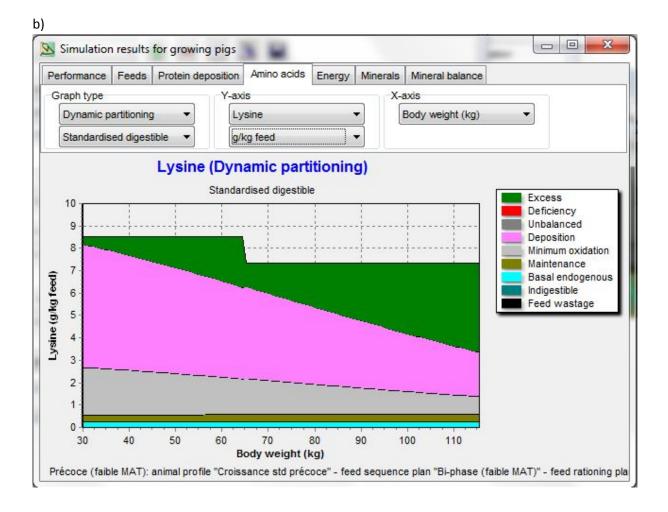
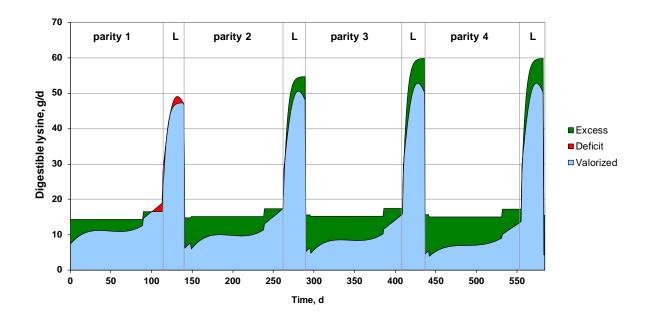
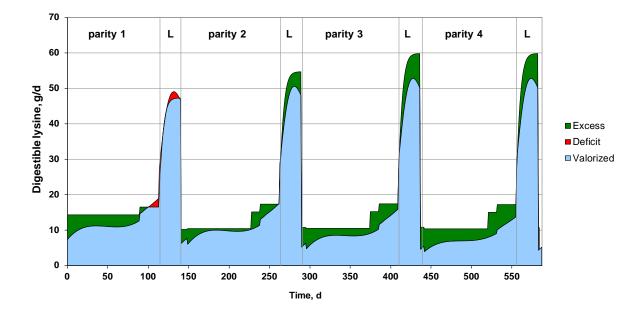


Figure 2. Simulated effect of different gestation feeding strategies on the utilization of ileal digestible lysine (a): one diet, (b): two diets in multiparous sows with a change at 80 d of gestation, (c): two diets mixed in adequate proportions to meet lysine and apparent digestible phosphorus requirements (from Dourmad et al., 2015a).



a)





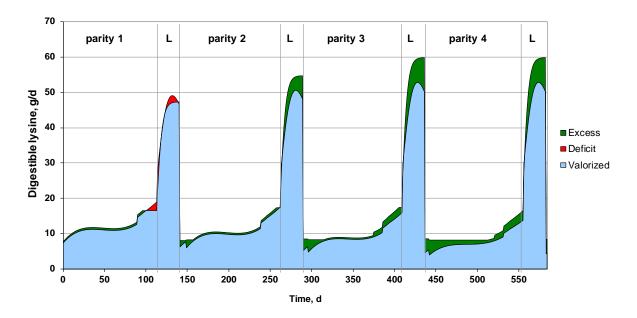
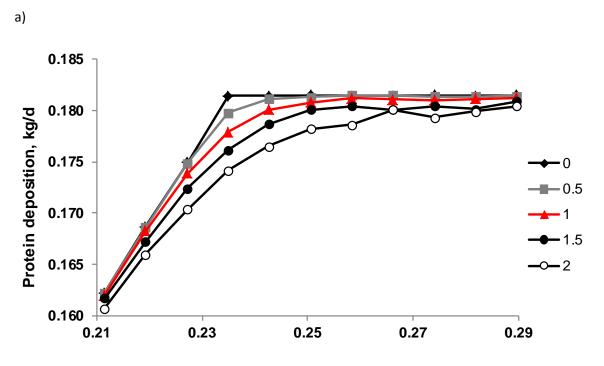


Figure 3. Effect of growth parameters variability between individual pigs (0, 0.5, 1, 1.5 et 2 times the variance of a reference population) and quantity of ingested protein on daily protein deposition (a) and percentage of under-fed pigs (b) for 50 kg BW pig population (from Pomar et al., 2005).



Balanced protein intake, kg/d

b)

