

GrazeIn: a model of herbage intake and milk production for grazing dairy cows. 1. Prediction of intake capacity, voluntary intake and milk production during lactation

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Abstract

The prediction of both food intake and milk production constitutes a major issue in ruminants. This article presents a model predicting voluntary dry matter intake and milk production by lactating cows fed indoors. This model, with an extension to predict herbage intake at grazing presented in a second article, is used in the Grazemore decision support system. The model is largely based on the INRA fill unit system, consisting of predicting separately the intake capacity of the cows and the fill value (ingestibility) of each feed. The intake capacity model considers potential milk production as a key component of voluntary feed intake. This potential milk production represents the energy requirement of the mammary gland, adjusted by protein supply when the protein availability is limiting. Actual milk production is predicted from the potential milk production and from the nutritional status of the cow. The law of response of milk production is a function of the difference between energy demand and actual energy intake, modulated by protein intake level. The simulation of experimental data from different feeding trials illustrates the performance of the model. This new model enables dynamic simulations of intake and milk production sensitive to feeding management during the whole lactation period.

Keywords: model, dairy cow, intake, milk production, lactation

Introduction

The economic, labour and environmental interests of grazing justify improving decision support systems for management of grazed systems with dairy cows. The purpose of the European Grazemore decision support system (Mayne *et al.*, 2004) is to help farmers and advisers manage grazing by simultaneously balancing pasture management and dairy herd performance. For this purpose, it is necessary to develop both a grass growth model and an intake and milk production model integrating the specificities of grazing management. Nevertheless, in Europe, dairy cows do not graze all year long and are very often fed with supplements (forage or concentrates) during grazing. Therefore, it is essential to build a general model of intake, able to predict intake, irrespective of diet. Forecasting intake is essential to predict both grass uptake by the cows at grazing, required to simulate the evolution of grass cover (Barrett *et al.*, 2005), and the supply of nutrients to the cow, required to estimate the consequences in terms of milk production. The model simulating food intake and milk production by grazing cows is presented in a series of three publications. This first article describes the concepts and the equations of voluntary food intake and milk production models. The second presents the model adaptation necessary to take into account grazing management (Delagarde *et al.*, 2011a). The internal and external validation of the whole model under grazing conditions is presented in the third article (Delagarde *et al.*, 2011b).

Intake prediction is essential to evaluate the diet of ruminants, particularly because the forage intake is very difficult, or impossible, for farmers to estimate at grazing. Combined with other systems to evaluate nutritional qualities of the diets, it makes it possible to analyse the benefits of supplements. The purpose of rationing, however, is not to express all the potential of

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production of a dairy cow, but rather to find a better compromise between the different goals of the system (profitability, workload, milk quality, environment, grazing management, etc.) (Dillon *et al.*, 2005). Consequently, this model does not aim to find the best diet for a cow, but rather to estimate how much it will produce according to the diet offered. Consequently, it requires modelling of mammary gland response to various nutritional situations, including the role played by the animal's body reserves. To date, no dynamic model is really able to simultaneously predict changes in intake, milk production and body reserves. The complexity of such a model is related to the strong interactions connecting these three entities and to the dynamic nature of their relations. Additionally, the significant number of parameters and data necessary to inform such a model make its use difficult for a decision support tool.

The general intake and milk production framework model is first described before the presentation of the different aspects of the model: (i) the theoretical model determining the potential milk production by the mammary gland, (ii) the model predicting voluntary dry matter intake, whatever the supplementation strategy, and (iii) the prediction of actual milk production. Finally, the last part presents an initial validation of the intake and milk production model with stall-fed cows from experiments performed with conserved diets.

Framework of the model

The model described here aims to predict the dynamic evolution of voluntary intake and milk production during the lactation of a dairy cow receiving a ration for which the feed characteristics are known.

The general structure of the model integrates the main interactions between food intake regulation, milk synthesis by the mammary gland and the regulation of body reserves (Figure 1). The capacity of the udder to synthesize milk acts as a 'pull force' in the system, attracting nutrients to the secreting cells to enable the synthesis of milk components. A model of mammary

gland milk synthesis capacity is developed in the next part to represent the notion of potential milk production. The amounts of food eaten are regulated by this mammary gland uptake and also according to other characteristics of the cow (age, body size, stage of lactation, stage of gestation, energy balance) and diet (composition of the diet and food quality). A model of intake capacity and dry matter intake, using the fill unit system developed by INRA (1989), is proposed in the second part. Intake provides the nutrients playing a role of a 'push force' to supply the udder with the metabolites necessary to perform the syntheses. The change in milk production owing to nutrient availability (energy and proteins) is described in the third part. In the model, the INRA feeding systems are used to calculate net energy (UFL system) and metabolizable protein (PDI system) supplies and requirements of the cow. Definitions of the main variables used in the voluntary intake and milk production models are given in Table 1.

Theoretical lactation curve model

Many lactation curve models have already been published (see reviews of Masselin *et al.*, 1987; Beever *et al.*, 1991). Most of them are designed to fit the dynamics of milk production and to forecast average milk production for cows under similar conditions.

These models do not, however, include feeding conditions as an input of the model to fully predict consequences for production. Generally, they tend to underestimate or overestimate lactation curve persistency if feeding management differs from the data used to estimate the model's parameters. The purpose of a lactation curve model is thus to simulate the potential lactation curve of a dairy cow, which is the functional capacity of the mammary gland to produce milk.

Such a model of the potential lactation curve is a physiological model similar to previous models (Neal and Thornley, 1983; Roguet and Faverdin, 1999). Moreover, many experiments (Faverdin *et al.*, 1998; Friggens *et al.*, 1998; V  rit   and Delaby, 1998; Delaby *et al.*, 2009) have tended to demonstrate that potential production is not largely affected by a long period of poor-quality feeding.

Model description

The principle of the model consists in the dynamic theoretical modelling of a population of secretory cells within the mammary gland (Figure 2). The model makes partial use of the modelling approach suggested by Neal and Thornley (1983) and its adaptation made by Roguet and Faverdin (1999). The model's time interval is the day and t is the time variable (in days after calving).

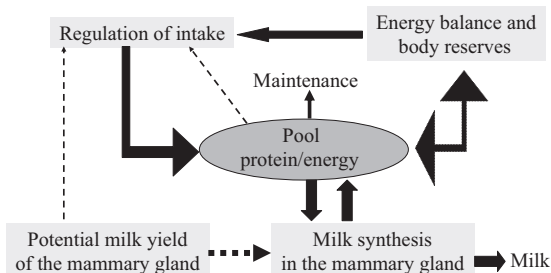


Figure 1 General framework of the food intake and milk production model.

Table 1 Definitions of the variables used in the GrazeIn model predicting voluntary intake and milk production of dairy cows.

Name	Unit	Description
Input		
Animal characteristics		
Parity		Primiparous or Multiparous (boolean)
DIM	Day	Days in Milk
MPMax	kg d ⁻¹	Maximum Milk Potential Production of the lactation
DInsF	Day	Days since last calving at fertilizing insemination
BCS	Scale 0–5	Body condition score
LW	kg	Live weight
Age	Month	age of the cow
WG	Week	Week of gestation
WL	Week	Week of lactation
Diet characteristics		
FVfi	LFU kg DM ⁻¹	Fill value of each forage <i>i</i> used (calculated or table values)
F% _i *		Proportion of each forage <i>i</i> per kg of DM offered (mixed diet)
C%*		Proportion of concentrate per kg of DM offered (mixed diet)
PDIE _i	g PDIE kg DM ⁻¹	Protein Value of each feed (calculated or table values)
UFL _i	UFL kg DM ⁻¹	Energy Value of each feed (calculated or table values)
Output		
DMI	kg d ⁻¹	Total Dry Matter Intake
pMP	kg d ⁻¹	Potential Milk Production
aMP	kg d ⁻¹	Actual Milk Production according to diet offered

*If some feeds are offered in fixed amounts, then these amounts must be added to describe the diet. The proportions of the different ingredients are recalculated by the model for the whole diet.

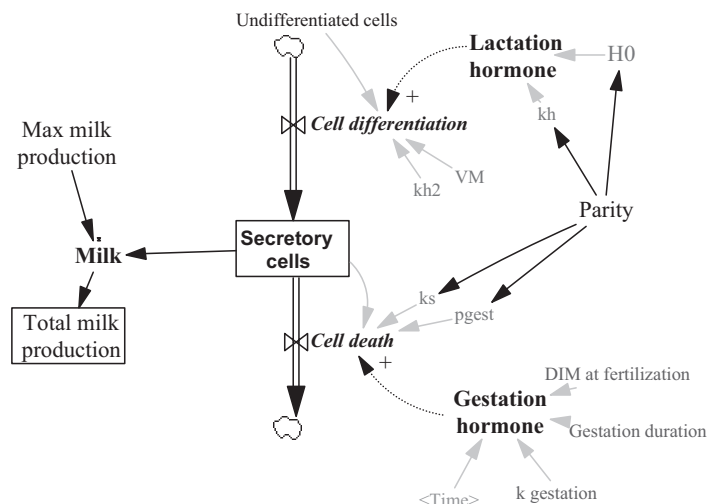


Figure 2 Diagram of the simplified model of potential lactation curve derived from the model of Neal and Thomley (1983) and of Roguet and Faverdin (1999). The shape of the lactation curve is driven by the number of secretory cells. This number depends on two processes: secretory cell differentiation controlled by a theoretical lactation hormone and secretory-cell death (or apoptosis). The cell-death process is more active in multiparous cows and during pregnancy, which is simulated in the model by the effect of a theoretical gestation hormone. Milk potential is modulated by the characteristic of maximum milk production of the cow. This parameter drives the milk secretion of secretory cells to predict daily milk production.

The model simulates lactation-curve dynamics based on the variation of an arbitrary number of secretory cells (*Secretory_cells*). New secretory cells are produced by a daily differentiation process (*cell_differentiation*), whereas the number of secretory cells disappearing is simulated by a death process (*cell_death*). The rates of both differentiation and death of secretory cells differ between primiparous and multiparous cows. Production potential does not appear in the number of cells but in the capacity of the secretory cells to produce milk.

Lactation starts at calving, with an initial number of secretory cells. During lactation, the udder differentiates new cells, in particular just after calving, and gradually some of these cells die throughout the lactation process. The number of secretory cells is obtained by integration of the following differential equation during lactation:

$$\frac{d(\text{Secretory_cells})}{dt} = \text{cell_differentiation} - \text{cell_death} \quad (1)$$

The initial theoretical amount of secretory cells is arbitrarily fixed at 2500 for primiparous and 3000 for multiparous cows to take into account a difference in mammary development because of parity.

Cell differentiation

The differentiation of secretory cells is directly related to a theoretical lactation hormone (*HL*, in g L^{-1}) modelled by a decreasing exponential function with *t*, the day in milk (Neal and Thornley, 1983). The initial value of *HL*

at the beginning of lactation (*H0*) and the rate of exponential decrease in this hormone (*kH*, in d^{-1}) differ between primiparous and multiparous cows. The values of *HL* are arbitrary and are not scaled on existing hormones.

$$HL = H0 \times e^{(-kH \times t)} \quad (2)$$

with *H0* = 0.5 and *kH* = 0.08 for primiparous cows, and *H0* = 0.8 and *kH* = 0.13 for multiparous cows.

The higher coefficient for multiparous cows indicates an earlier milk-production peak than that for primiparous cows (Figure 3a). The differentiation of new secretory cells is calculated using the equation of Neal and Thornley (1983). This process is modulated by the number of undifferentiated cells (*CU*), the maximum rate of differentiation *VM* (division $\text{cell}^{-1} \text{d}^{-1}$) and the constant *kH2* (g HL L^{-1}).

$$\text{Cell_differentiation} = \frac{VM \times CU \times HL}{kH2 + HL} \quad (3)$$

with *VM* = 0.155, *CU* = 1000 and *kH2* = 0.2

These coefficients are arbitrary, and their role is to describe the shape of the lactation curves of well-fed dairy cows.

Cell death

Cell degeneration is a function of the number of secretory cells and of the stage of gestation of the cow. The model of Neal and Thornley (1983) did not

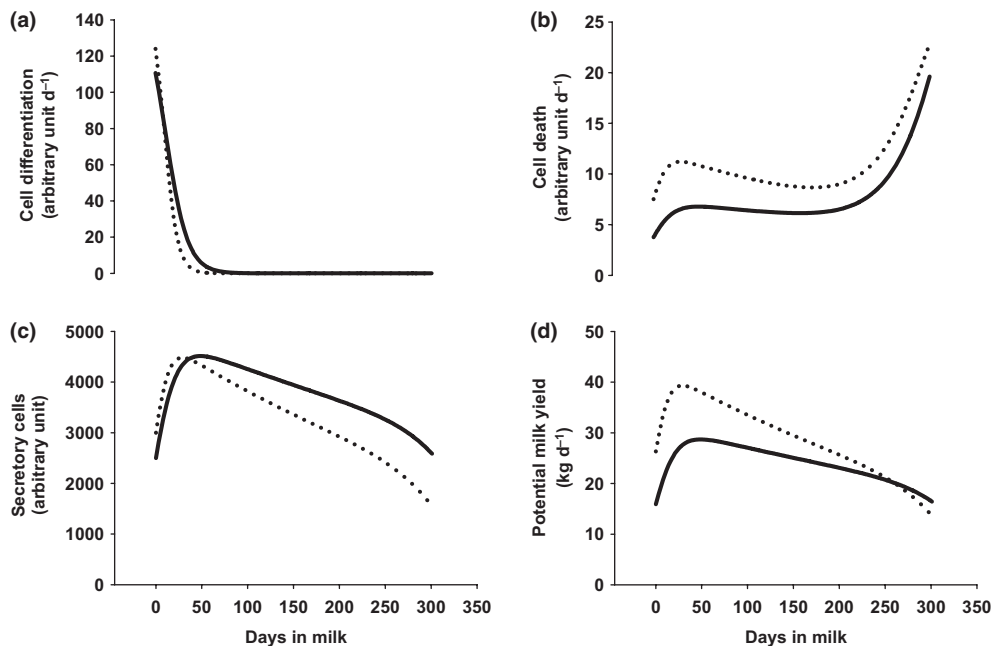


Figure 3 Changes in secretory cells [differentiation (a), death (b), total number (c)] and potential milk production (d) simulated by the model for primiparous (solid line) and multiparous (dotted line) cows during the lactation.

consider the stage of gestation. A previous model of the lactation curves (Coulon and Pérochon, 1998) clearly showed an effect of the stage of gestation on the persistency of the lactation curve. This function is useful to simulate the drop of milk production in late gestation, but also to better simulate the lactation curve of non-pregnant cows with long lactation.

The effect of the theoretical gestation hormone (HG , in $g\ L^{-1}$) is a function of days in milk determined in a manner symmetrical to that of the lactation hormone, but fixed to reach $HG = 1$ at the next calving. The average duration of gestation was fixed at 270 days. The model calculates the stage of gestation starting from the day of fertilizing insemination ($DInsF$, in days after calving).

$$HG = e^{-kg \times (270 - t + DInsF)} \quad (4)$$

with $kg = 0.0305$, value obtained from an optimization series of a previous model (Roguet and Faverdin, 1999).

The death of cells, $death$, is proportional to the number of secretory cells. The basal rate of death is ks (in d^{-1}). This rate is increased by the gestation hormone effect with a coefficient pg . The coefficient rates vary with cow parity. The death of cells is calculated by the formula:

$$Cell_death = Secretory_cells \times (ks + pg \times HG) \quad (5)$$

with $ks = 0.0015$ and $pg = 0.02$ for primiparous cows, and $ks = 0.0025$ and $pg = 0.04$ for multiparous cows.

These values are rounded average values, obtained by calibration on individual cow data of two experiments in which the cows received a complete and good-quality ration throughout lactation. The cell death rate is higher for multiparous cows and agrees with the frequently made observation of the lower persistency of the lactation curves of multiparous cows compared to primiparous cows (Figure 3b and c).

Milk synthesis

The number of secretory cells is only used to simulate the shape of the milk production curve (Figure 3d) and is not affected by the genetic merit of the cow. To describe different milk potential production, the number of secretory cells is multiplied by a coefficient of milk synthesis (CMS , in $kg\ d^{-1}\ cell^{-1}$):

$$pMP = Secretory_cells \times CMS \quad (6)$$

To fit most of the lactation curves, CMS values vary between 0.04 and 0.11. However, synthesis amplitude should be characterized by easy-to-obtain general parameters that can be milk production at peak or cumulated over 305 days. As CMS is not easy to relate directly to milk potential, the model is reparametrized to use daily milk production at the peak of

production, $MPMax$ (in $kg\ d^{-1}$), as a characteristic of lactational potential. A regression between CMS and the observed $MPMax$ predicted by the model was built for primiparous and multiparous cows and showed a good relationship ($R^2 = 0.997$). The following equation makes it possible to obtain this result with good accuracy:

$$CMS = \frac{(2.2 \times MPMax + 0.44)}{10000} \quad (7)$$

To estimate $MPMax$ from 305 days milk production, a set of whole-lactation simulations was carried out using different parities and $MPMax$ values with the day of fertilizing insemination fixed at 100. These simulations indicate a very close relationship between the production peak and 305 days milk production ($R^2 = 0.999$), the value of the regression coefficient at the origin being not significantly different from 0. The $MPMax$ values can be calculated by dividing the 305 days milk production by 258 for primiparous cows and by 226 for multiparous cows. Thus, it is possible to parameterize milk potential of a cow using either $MPMax$ or 305 days milk production.

This model of the theoretical curve of lactation forecasts potential milk production with only few inputs: day of lactation, parity and a potential production at peak (or total 305 days milk production). A simple program in VBA (Microsoft®) is given in Appendix 1 to create a new function of this model in an Excel spreadsheet (Microsoft®).

Voluntary intake model

Many models have been developed to predict voluntary dry matter intake (VMDI) in practice (see reviews by Faverdin, 1992; Ingvarsen, 1994). They can be approximately grouped into three main classes: (i) the equations in which VMDI is directly predicted using multiple linear regressions mixing both animal and diet characteristics, (ii) models based on the most limiting of physical or metabolic intake regulation and (iii) fill unit systems mixing both physical and metabolic parameters by means of different satiety values of feeds. Multiple regressions do not allow the simulation of a large diversity of animal and feeding management. Models based on the most limiting of physical or metabolic intake regulation are conceptually interesting, but have some difficulty in taking into account all the factors involved in DMI regulation with these two limiting factors (Faverdin *et al.*, 1995). The FU systems, based on substitution between feeds, are more empirical and require more *in vivo* measurements, but fit better to a large diversity of situations.

The choice was thus made to retain the principle of the INRA fill unit system (Dulphy *et al.*, 1989), more

flexible, as a basis for the GrazeIn model and to adapt it to grazing dairy cows. A major argument was the ability of this system to take into account a great diversity of feeding systems from data that are easy to obtain in practice. Other INRA energy value (UFL) and protein value (PDI) systems, established in coherence with the fill unit system were also retained to predict food value, nutritional requirements and expected milk responses.

Principles of the fill unit (FU) system

The principle of the FU system is simple and has previously been described (Dulphy *et al.*, 1989), together with its use for dairy cows (Coulon *et al.*, 1989). It consists in separately predicting the intake capacity of ruminants and the fill value of food with a common unit, not the *kg* of *DM*, but the FU. The system considers that the intake capacity (*IC*) is equal to the sum of the amounts of dry matter of each food eaten (DMI_i) multiplied by their fill value (FV_i) if one of the foods is consumed *ad libitum*:

$$IC = \sum_i DMI_i \times FV_i \quad (8)$$

Thus, from Equation 8, it is easy to calculate the unknown DMI_u of a forage (or a mixture of feeds in fixed proportions) offered *ad libitum*, if its fill value (FV_u) and the amount and characteristics of the *i* other feeds in fixed amount are known, using Equation 9. The fill unit system is not able to predict VDMI of several feeds offered *ad libitum* with an unknown proportion because of the difficulty to predict the choice.

$$DMI_u = \frac{IC - \sum_i DMI_i \times FV_i}{FV_u} \quad (9)$$

The fill value of a feed is an inverse function of its 'ingestibility'. The intake capacity is a function of animal characteristics alone and the forage *FV* is a function of the forage characteristics alone (species, stage, chemical composition). The concentrate *FV*, on the other hand, is not constant and varies according to the substitution rate and the energy balance of the dairy cow (Faverdin *et al.*, 1991). Therefore, in dairy cows, the regulation of intake related to energy constraints is mainly described in the FU system through the variations of concentrate fill value. However, the metabolic regulation is not only attributed to energy supply, but also to protein supply (Faverdin *et al.*, 2003). In this evolution of the fill unit system, the availability of metabolizable protein could affect intake capacity (see later). As these energy and protein supplies depend on *DMI* and affect *IC*, which, in turn, is used to calculate

DMI, the calculation of *DMI* requires an iterative procedure.

Intake capacity

The previously published model of intake capacity (Coulon *et al.*, 1989) was very simple, taking into account only actual milk production, live weight and parity of the cows. A new equation is proposed to take into account additional effects, but keeping coherent values with the previous equation. Actual milk production (*aMP*), however, is highly dependent on the feeding conditions and sometimes does not reflect the potential milk production (*pMP*). The model now proposed distinguishes a cow's potential milk production, taking into account its genetic merit and its physiological characteristics. The submodel of intake capacity is built on three main factors known to affect intake capacity: live weight (*LW*), potential milk production modified by metabolizable protein intake (see Equation 20; *MPprot*), the body condition score (*BCS*, estimated by a visual assessment on a scale of 0–5). The *MPprot* largely depends on *pMP*, but could be modified if metabolizable protein supply does not satisfy the protein requirement of *pMP*. Thus, the protein regulation of feed intake is represented in the model by the effect of *MPprot*. This intake capacity is also corrected by three indices to take into account changes in intake capacity with the age and the physiological state of the cow: *IL*, an index of lactation, function of the week of lactation (*WL*), *IG* an index of gestation, function of the week of gestation (*WG*) and *IM*, an index of maturity, function of the age of the cow in months (*age*) (Figure 4). After calving, the development of digestive capacity and the use of body reserves, related to the homeorhesis of early lactation (Faverdin and Bareille, 1999), tend to delay the increase in intake capacity and explain the specific index *IL*. The stage of lactation modifies the intake capacity with the *IL* index, but also by way of *pMP*, used to calculate *MPprot*, and variation in *BCS*.

$$IC = (13.25 + (LW - 600) \times 0.02 + MPprot) \times 0.15 + (3 - BCS) \times 1.5 \times IL \times IG \times IM \quad (10)$$

$IL = a + (1 - a) \times (1 - e^{-0.22 \times WL})$, with $a = 0.43$ for primiparous and $a = 0.6$ for multiparous cows

$$IG = 0.8 + 0.2 \times (1 - e^{-0.25 \times (40 - WG)})$$

$$IM = -0.1 + 1.1 \times (1 - e^{-0.08 \times age})$$

The coefficients of *IC* equation are centred to keep the reference of *IC* for lactating dairy cows of the previous equation (17 LFU for an adult mid-lactating dairy cow producing 25 kg of milk with a 600-kg *LW*). The coefficients of *LW* and *BCS* were estimated using

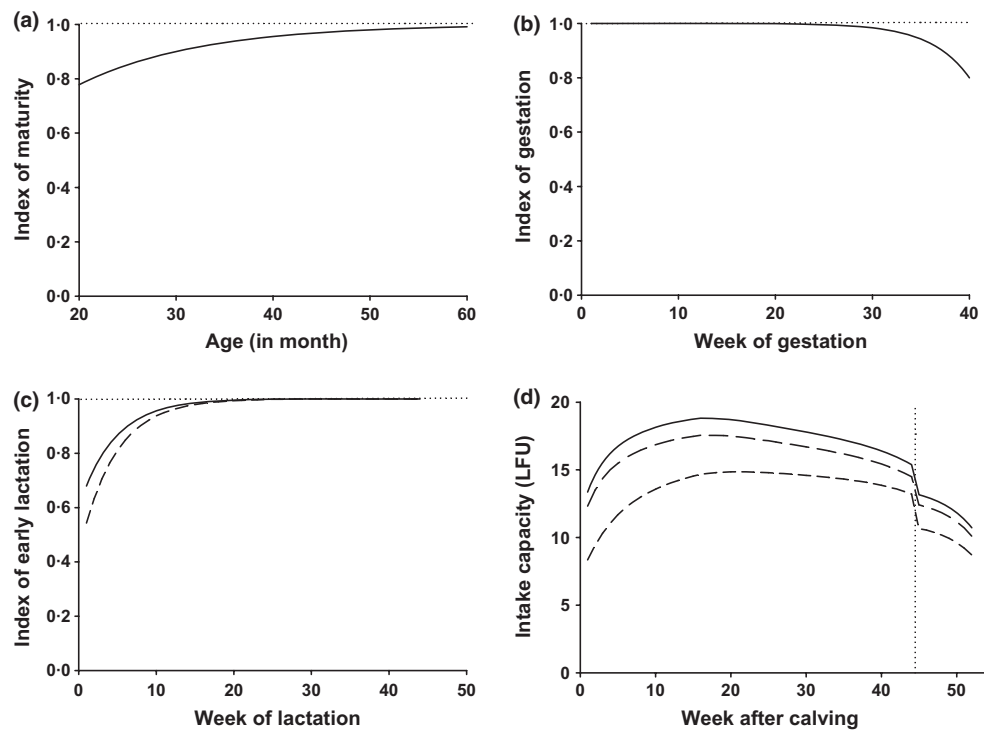


Figure 4 Changes in the three intake capacity correction indices for (a) maturity, (b) gestation and (c) lactation with primiparous (---) and multiparous cows (—). Figure (d) summarizes changes in intake capacity (in fill units, LFU) over three consecutive lactations (----- first lactation, --- second lactation, — third lactation) for a cow with a 9000 kg potential of milk production per lactation in the third lactation, the dotted vertical line indicating the beginning of the drying-off period.

different experiments with dairy cows fed on the same diet in which these two variables were measured simultaneously with feed intake. The average values of $0.02 \text{ LFU kg}^{-1} \text{ LW}$ and $-1.5 \text{ unit}^{-1} \text{ BCS}$ corresponding to the average values between trials were finally kept for this equation.

The value of 0.15 LFU kg^{-1} potential milk was derived from trials using cows with different genetic merit at grazing (Horan *et al.*, 2006) and after adjustment of differences in *LW* and *BCS*.

Three indexes are introduced to better simulate the dynamic evolution of the *IC*. The effect of age was previously described by a fixed effect differing between primiparous and multiparous cows (Coulon *et al.*, 1989). However, the effect of age should be continuous from first calving to adult cows. So the index *IM* is introduced to take into account the effect of maturity, which is not only explained by *LW* and *MP*. This equation is adjusted on data from a long-term trial (Coulon and Ollier, 1996) with an asymptotic regression model (Faverdin *et al.*, 2007). The *IL* differs from 1 only in early lactation, whereas *IG* differs from 1 only in late gestation (late lactation and dry period). For *IL*, the

same type of asymptotic regression model is used to describe the differences observed in early lactation with an INRA database (unpublished). Fewer data are available to describe the dry period during which restricted feeding is often used. Hayirli *et al.* (2003) described variations observed with an asymptotic model. The 0.25 value of the exponent coefficient corresponds to the average of proposed values for primiparous and multiparous cows in this study.

Forage fill value

Each forage is characterized by only one fill value (*FV*) expressed in $\text{LFU kg}^{-1} \text{ DM}$ for dairy cows (lactating fill unit). The fill value of forage is an inverse function of its 'ingestibility' and is calculated by the ratio of intake of the reference forage to voluntary dry matter intake of the considered forage (expressed in $\text{g DM kg}^{-1} \text{ BW}^{0.75}$). The reference value of 1 LFU corresponds to forage consumed by a dairy cow at a rate of $140 \text{ g DM kg}^{-1} \text{ BW}^{0.75}$. As a result of the definition of the *FU* system, the rate of substitution between forages expressed in LFU is constant and $=1$, but expressed in

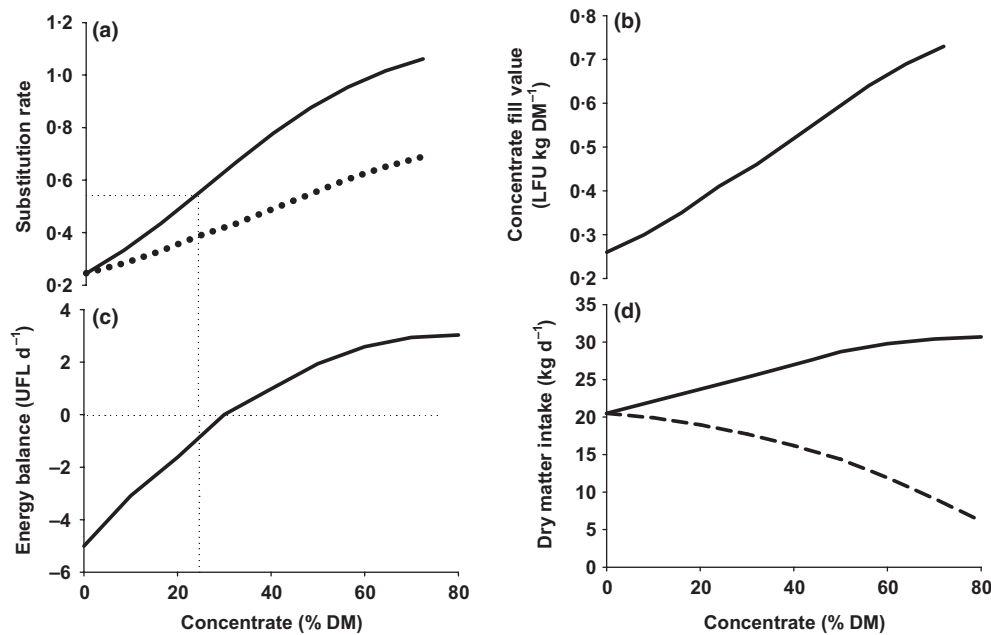


Figure 5 Predicted effects of the proportion of concentrates in the diet on marginal (solid line) and global (dotted line) substitution rate (a), concentrate fill value (b), energy balance (c) and total (solid line) and forage (dotted line) dry matter intake (d) according to the fill unit system for dairy cows. The marginal substitution rate function is always centred on 0.55 for the proportion of concentrates required to equilibrate the energy balance. The concentrate fill value is a function of the integral of the marginal substitution rate.

DM, it equals the ratio between the two forage fill values. For example, if a cow with a *IC* of 15 LFU is fed with a hay whose *FV* is 1.15 LFU, predicted *DMI* is 13.04 kg (15/1.15). If hay offered is limited to 8 kg of DM and straw with a *FV* of 1.6 LFU is offered *ad libitum*, predicted *DMI* of straw is 3.63 kg ((15–8 × 1.15)/1.6, see Equation 9) and total *DMI* is 11.63 kg. The *FV* of the forages were obtained empirically by many measurements of voluntary intake in sheep and cattle using a standard procedure. More than 2400 different forages were tested, and the average forage *FV* are given in published tables (INRA, 1989). Forage *FV* can also be predicted using the chemical composition of the forage (crude fibre, crude protein and dry matter concentration) (Baumont *et al.*, 2007). In the case of fresh forages, specific equations for each species (grasses and legumes) make it possible to calculate the *FV*. For conserved forages, the food values could be easily obtained in INRA Tables (INRA, 1989) or with specific equations using either *FV* of fresh forage or directly from chemical composition.

Concentrate fill value

Contrary to the forage fill value (*FVf*), the concentrate fill value (*FVc*) is variable, taking into account the metabolic regulation of intake. Mathematically, it is a

function of the global substitution rate (*GSR*) observed between forages and concentrates (Figure 5).

$$FVc = FVf \times GSR(C\%) \quad (11)$$

It is, however, difficult to find experiments with lactating dairy cows comparing diets with high amount of concentrates to diets with forage alone, which is necessary to estimate *GSR*. On the contrary, a lot of experiments compare different amounts of concentrates, enabling the calculation of a marginal substitution rate between the different amounts of concentrate. Consequently, the concentrate *FV* is generated by a logistic model of the marginal substitution rate (*mSR*) simulating the increase in substitution rate as the energy balance increases (Dulphy *et al.*, 1989; Faverdin *et al.*, 1991). The *mSR* and *GSR* are calculated from the proportion of concentrate *C%* in the diet and *UFLf* and *UFLc* as the average net energy values (UFL) of forages and concentrates respectively, by the formula (Figure 5):

$$mSR(C\%) = \frac{k}{1 + d \times e^{b \times (R\% - C\%)}} \quad (12)$$

where $k = \frac{UFLc}{UFLf}$, $d = \frac{k}{0.55} - 1$, and $b = 4.5 \times UFLf$

$$GSR(C\%) = \frac{1}{C\%} \times \int_0^{C\%} mSR(C\%) \times dC\% \quad (13)$$

An algebraic solution to the integral (Equation 13) can be used to calculate *GSR* easily:

$$GSR(C\%) = k \times \left[1 + \frac{1}{(b \times C\%)} \times \ln \left(\frac{d \times e^{(b \times (R\% - C\%))} + 1}{d \times e^{(b \times R\%)} + 1} \right) \right] \quad (14)$$

$R\%$ represents the theoretical proportion of concentrate required to achieve a null energy balance. It could be negative with very good forages and low-producing cows, but it is limited to a minimum value of -0.2 . The INRA net energy system (unit for dairy cows is $UFL = 7.1$ MJ of net energy) is required to determine the $R\%$ value, mainly to estimate the energy requirements (UFL_{req}) of the cows and the net energy intake.

$$R\% = \frac{IC \times \frac{UFL_f}{FVf} - \frac{UFL_{req}}{CorUFL}}{\frac{UFL_{req}}{CorUFL} \times (GSR(R\%) - 1) - \frac{IC}{FVf} \times (UFL_c - UFL_f)} \quad (15)$$

with $CorUFL$ the coefficient of correction of net energy because of the digestive interactions and the non-additivity of UFL values as previously published by INRA (1989):

$$CorUFL = 1 - \frac{6.3 \times C\%^2}{\sum_i DMI_i \times UFL_i} + 0.002 \times \sum_i DMI_i \times UFL_i - 0.017 \quad (16)$$

This correction of net energy with $CorUFL$ is because of the decrease in diet digestibility associated with the increase in DMI and with the increase in concentrate proportion in the diet.

The cows' energy requirements are calculated in UFL using the equation based on the INRA UFL net energy system (INRA 1989) and adapted to take into account the role of body reserves mobilization in early lactation:

$$UFL_{req} = (0.041 \times LW^{0.75}) \times act + 0.44 \times (4\%FCMP_{prot}) + 0.0315 \times e^{(0.116 \times WG)} + UFL_{mob} + UFL_{growth} \quad (17)$$

Where

- act is a coefficient of correction of the energy requirement for maintenance, $act = 1.2$ for grazing cows, 1.1 for loose housed cows and 1.0 for stall-fed cows.
- $4\%FCMP_{prot}$ is the MP_{prot} corrected for 4% fat content ($kg\ d^{-1}$)
- WG , the week of gestation, to calculate energy needs for gestation (mainly during the last 3 months of gestation) (week of gestation, 0 before fertilizing insemination)
- UFL_{mob} is negative and represents the intrinsic energy mobilization of body reserves during the beginning of lactation (in UFL , see later).

- UFL_{growth} : For cows younger than 40 months, an additional energy requirement in UFL for growth is required using a function of age (in months):
 $UFL_{growth} = 3.25 - 0.08\ age$

The $GSR(R\%)$ equation is a particular case of the general equation $GSR(C\%)$

$$GSR(R\%) = -\frac{k}{b \times R\%} \ln \left(1 - 0.55 \times \frac{1 - e^{(-b \times R\%)}}{k} \right) \quad (18)$$

The precision of DM intake prediction is suitable to compare diets with different proportions of concentrate as long as acidosis phenomena do not affect intake. This model, however, complicates the simulation process, because the energy supply is a function of DMI intake and DMI prediction requires a value for $GSR(R\%)$ predicted using energy intake. Thus, the model needs a calculation algorithm to converge towards a steady value, but the convergence is very rapid.

This mobilization of body reserves is normally induced by insufficient energy supply but also by the modification of the hormonal profile of the cows in early lactation (Faverdin and Bareille, 1999). This mobilization in early lactation is much more sensitive to animal characteristics than to diet composition. The expected mobilization of body reserves increases with maximum milk production and with the body condition score at calving, but decreases with the stage of lactation as simulated in Faverdin *et al.* (2007) using a large database of 680 cows in early lactation.

$$if > 0, UFL_{mob} = -1 + [1.33 \times (a + (0.47 \times MP_{Max}) + (1.89 \times BCS))] \times (e^{-0.25 \times WL} - e^{-WL}) \quad (19)$$

with $a = -9.5$ for primiparous and $a = -13.2$ for multiparous cows, otherwise $UFL_{mob} = 0$

If the energy supplied by the mobilization of body reserves in early lactation is not considered as available energy, the calculated substitution rates would be very low. Experimental data suggest that, during early lactation, the substitution rates of concentrates are not lower than in mid lactation with the same diet in spite of higher energy deficit (Faverdin *et al.*, 2007).

Prediction of milk production

Milk production is a function of the potential production of milk and of the amount of energy and protein supplied. Potential milk production drives the energy requirement for the milk synthesis by the mammary gland. This energy requirement is reduced when the amino acids required for the synthesis of milk proteins are not supplied in sufficient amounts. The PDI system

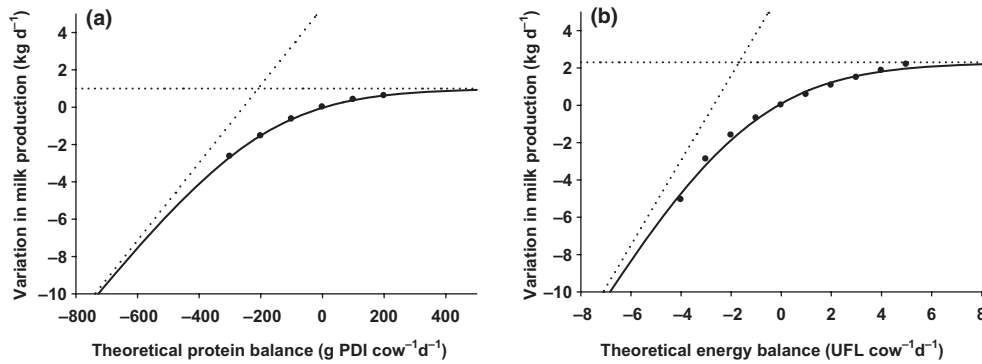


Figure 6 Predicted variation in milk production according to (a) the variation in theoretical protein balance (PDI intake – PDI requirements for maintenance and potential milk production) and (b) the variation in theoretical energy balance (energy intake – energy requirements for maintenance and milk synthesis possible with PDI intake). These models were calibrated on the equations of Vérité and Peyraud (1989) for protein, and Coulon *et al.* (1989).

was used to estimate metabolizable protein supply and requirements (INRA, 1989) and to calculate the protein balance ($PDIE_{bal}$) to assess the level of protein availability for milk synthesis. Vérité and Peyraud (1989) defined a response curve of milk production to protein availability using a set of protein nutrition experiments with no change in energy intake. This curve follows a law of diminishing returns. It was readjusted in this work using the model suggested by Koops and Grossman (1993) to simulate a smoothed transition between two linear segments (Figure 6). This option was used to enable simulating milk response in extreme situations with a minimum of theoretical assumptions, whereas no data were available to fit the model in this situation. The slope of the first linear segment is calculated according to the milk protein requirement of the PDI system (INRA, 1989), i.e. 48 g of PDI per kg of milk. The second segment assumes that, with a high excess of protein, there is no additional possible increase in milk production owing to a supplement of protein (the slope is nil).

$$MP_{prot} = pMP + 5.34 + 2.08 \times PDIE_{bal}/100 - 3.76 \times \ln \left[\frac{1 + e^{PDIE_{bal}/100 + 2.09}}{1.81} \right] \quad (20)$$

With

$$PDIE_{bal} = \sum_i PDIE_i \times DMI_i - (3.25 \times LW^{0.75} + 48 \times pMY) \quad (21)$$

The pMP driving the intake capacity is readjusted according to the availability of proteins. The change in pMP potentially synthesized by the mammary gland according to protein availability enables the model to partly simulate the positive effects of protein nutrition

on appetite and the increase in this effect over time (Rico-Gómez and Faverdin, 2001; Faverdin *et al.*, 2002, 2003). Consequently, protein supply and MP_{prot} could be affected. This requires that iterative calculations be conducted until convergence.

Actual milk production (aMP) is also predicted from the cow's energy balance. The response of milk production is a function of the difference between energy demand (function of the pMP modulated by the protein intake) and predicted energy intake. This law of response of actual milk production to energy availability was modelled using the data synthesized by Coulon and Rémond (1991) and was readjusted, as for proteins, using the model of Koops and Grossman (1993) (Figure 6). The slope of the first linear segment is calculated according to the milk energy requirement for milk production in the UFL system (0.44 UFL kg⁻¹ of milk, i.e. 2.27 kg of milk UFL⁻¹). The second segment is nil, assuming that with a high excess of energy, there is no additional increase in milk because of extra energy.

$$aMP = MP_{prot} + 6.13 + 2.27 \times UFL_{bal} - 5.47 \times \ln \left[1 + e^{\frac{UFL_{bal} + 1.69}{2.41}} \right] \quad (22)$$

With

$$UFL_{bal} = corUFL \times \sum_i UFL_i \times DMI_i - UFL_{req} \quad (23)$$

These equations allow the prediction of different milk production responses to similar energy supplies according to the genetic merit of the cow.

Validation of the model

The validation of this model for food intake and milk production in grazing situations is fully included in

the third article concerning this model (Delagarde *et al.*, 2011b). The objective of this section is to evaluate the ability of the model to predict the dynamics of intake and milk production in lactating groups of cows managed with different strategies of reproduction or fed with different diets. The actual (A) and predicted (P) weekly intake and milk production of experimental group of cows were compared using the mean-squared prediction error (MSPE), regarded as the sum of three components, namely mean bias, line bias and random variation (Bibby and Toutenburg, 1977):

$$\text{MSPE} = 1/n \sum (A - P)^2 = (\text{Am} - \text{Pm})^2 + \text{SP}^2(1 - b)^2 + \text{SA}^2(1 - R^2)$$

where n is the number of A and P pairs of groups compared, Am and Pm are the means of A and P respectively, SA^2 and SP^2 are the variances of A and P respectively, b is the slope of the regression on A upon P, R^2 is the correlation coefficient of the regression of A upon P.

Positive or negative mean bias ($\text{Pm} - \text{Am}$) indicates overall over or underestimation by the model respectively. The line bias [$\text{SP}^2(1 - b)^2$] is the deviation of the slope of the regression of A upon P from unity. A large line bias is mainly indicative of inadequacies in model structure. Mean bias, line bias and random variation are presented below by their proportional contribution to the MSPE (Rook *et al.*, 1990). The mean prediction error (MPE), indicating the average precision of the prediction, is the square root of MSPE. The relative MPE

(rMPE) is calculated by dividing MPE by the mean actual value Am.

Validation of potential milk production

It is difficult to validate a theoretical model of potential milk production, because cows are rarely fed at the optimum level throughout the entire lactation period. We compared observed changes in production with primiparous or multiparous cows fed with good-quality diets during a complete lactation period, with lactation simulated by the theoretical model. A validation attempt consisted of comparing the model to a large set of lactations with Holstein cows managed under good conditions for expressing their milk potential, which is often the case in North America. Jamrozik *et al.* (1998) published data on persistency of milk production of Holstein cows having calved in 1995 in Canada. The data presented were compared (Table 2) to the outputs obtained using the theoretical model of potential lactation by adjusting the input variables (milk at peak) so that the production of milk on day 60 coincided with the observations of Jamrozik *et al.* (1998). There was a good fit between the model data and the values reported by these authors, allowing us to think that this model can be used without too much risk to simulate potential lactations.

Our model assumes increased apoptosis of mammary secretory cells during gestation that has not, as yet, been effectively demonstrated, in spite of preliminary unpublished results in favour of this theory. This

Table 2 Comparison of lactation data collected by Jamrozik *et al.* (1998) with Canadian cows having calved in 1995 ($n = 85\,414$) to those obtained with the theoretical model.

	Lactation 1		Lactation 2		Lactation 3	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
Production at day 60 (kg)*	28.3	28.3	35	35	37.5	37.5
Production at day 280 (kg)	20.1	19.4	18.8	18	19.2	19.3
305 days production (kg)	7452	7310	8461	8339	8934	8943
Cumulative production between						
Days 60 and 280 (kg)	5399	5336	5991	5872	6329	6298
DIM at peak	53	51	40	30	41	30
½ days between 5 and 305†	139	140	127	126	125	126
½ days between 60 and 305†	160	160	153	153	152	153
Model parameters						
Parity	1		2		2	
Milk at peak (MPMax)	28.5		37.0		39.7	
DIM at fertilization (DinsF)	90		90		90	

*The MPMax values of the model were calculated to obtain the same production at day 60 as the observed values.

†The criterion '½ days between I and J' defined by the authors corresponds to the day of lactation for which the cow reaches 50% of its production of milk cumulated between day I and J.

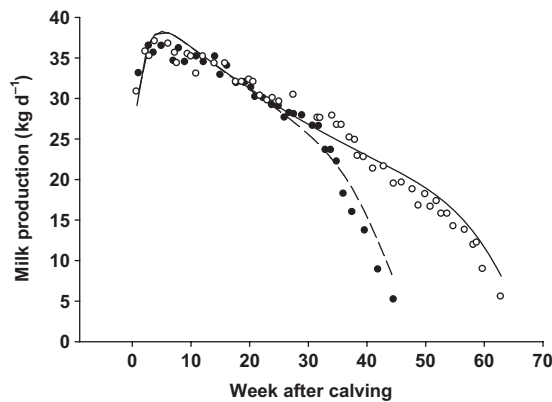


Figure 7 Comparison of observed (symbols) and simulated (lines) milk lactation curves of two herds inseminated either in early lactation (black symbols, dashed line) or in mid lactation (open circles, solid line) (data from Bertilsson *et al.*, 1997).

approach could be very efficient for simulating the impact of delayed insemination on the lactation curve. To validate this aspect, the model was compared to the data published by Bertilsson *et al.* (1997), comparing two herds inseminated either in early lactation or 5–6 months later. In their trial, the persistency of the lactation curve was greatly affected by gestation (Figure 7). The model is able to describe this impact of pregnancy on milk production with a high correlation ($R^2 = 0.97$) and a low standard deviation (1.51 kg d^{-1}). The average MPE of the model (Table 3) was 1.57 kg d^{-1} , which corresponds to a rMPE of 0.059, very similar for the two groups of cows (normal 0.057, late pregnancy 0.060), with 90% of the MSPE because of random effect.

Validation of intake and milk production changes induced by diet characteristics

This model is one of the first to incorporate not only the effect of roughage characteristics, but also the effect of protein and concentrate effect on intake and milk production simultaneously. To evaluate the sensitivity of this model to the diet composition for predicting DM intake in early lactation, the predictions at the beginning of lactation were compared to experimental data using two experiments testing the interaction of protein and concentrate content in complete diets during early lactation. The first experiment (briefly described in Faverdin *et al.*, 1998) was a 2×3 factorial design (20 and 40% of concentrate \times 85, 100 and 115 g of PDIE UFL^{-1}) with maize silage as forage (Figure 8). The second experiment (Faverdin *et al.*, 2002) was a 2×2 factorial design (25 and 45% of concentrate \times 92 and 110 g of PDIE UFL^{-1}) with grass silage and hay as forages (Figure 9).

In both trials, the model tends to better predict intake and milk production with the high protein diet either at low or high concentrate levels. The two trials indicate that the model of intake is sensitive to diet protein content by way of *MPprot* and the effects are, in trend, similar to experimental data in mid lactation. The MPE of VDMI with the model (Table 3) for the two trials ($n = 144 \text{ weeks} \times \text{groups}$) is 1.34 kg d^{-1} , which corresponds to a satisfying rMPE of 0.070. The mean bias is low in any case, with no effect of trial, parity nor stage of lactation on prediction accuracy. However, the prediction of milk production is less accurate. The average MPE for milk production is high for the two experiments (4.35 kg d^{-1}) with high rMPE (0.143) and mean bias (2 kg d^{-1}). Prediction accuracy is lowest in early lactation and in primiparous cows (rMPE of 0.185) with a high mean bias (40–50% of MSPE). We hypothesize that the increase in mobilization of body reserves to supply energy deficit for milk production in low-energy diets is not sufficiently considered by the model to explain the milk response. The prediction of the milk production in mid lactation (weeks 8–15) is much better (MPE = 2.78 kg d^{-1} and rMPE = 0.091).

An evaluation of the model on complete lactations with different feeding strategies is also presented using the experiment of Friggens *et al.* (1998). In this experiment, cows were offered poor-quality or good-quality mixed diets throughout the lactation period, or with a cross-over design at mid lactation (Figure 10). The same milk potential was assumed for the four treatments. Despite the small cow groups and low available information to define all the input variables required by the model, the simulated lactation curves describe the general trends observed in their experiment. The MPE of VDMI prediction (Table 3) is low, i.e. 1.02 kg d^{-1} for all groups, rMPE averaging 0.051 with a high random variation (88% of MSPE) compared to mean bias and line bias. The precision of the prediction is, of course, better with a good diet during the whole lactation (rMPE of 0.046) than when a poor diet was fed in the first part of lactation (rMPE of 0.106). The prediction of milk production for the complete lactation is much better than in early lactation experiments with a low MPE (2.39 kg), low rMPE (0.083) and low mean bias. With the good-quality diet during the whole lactation, the accuracy of the milk production prediction is high (MPE = 1.29 kg d^{-1} and rMPE = 0.039), whereas prediction of milk production is less accurate with the poor-quality diet in early lactation. The lactation curves simulated by the model appear too flat for cows with poor-quality diets. This model is able to describe the consequences of changes in diet protein and energy content on the shape of dry matter intake curve and, to a lesser extent, of lactation curves, but

Table 3 Precision of the prediction of the GrazeIn model for DM intake and milk production with different experiments using cows fed total mixed ration with conserved forage and concentrate either in early lactation or during a complete lactation.

Set of experiment	Actual (A)	Regression of A upon P				Bias (P-A)	MPE (kg d ⁻¹)	Proportion of MSPE			
		Origin	Slope	s.d.	R ²			Bias	Line	Random	rMPE
Early lactation (2 experiments with N × E interaction, Faverdin <i>et al.</i> , 1998, 2002)											
Total DM intake (kg d ⁻¹)											
2 trials	19.07	3.80	0.80	1.10	0.89	0.00	1.34	0.00	0.34	0.66	0.070
Primiparous cows	16.70	3.04	0.83	1.03	0.81	-0.33	1.16	0.08	0.13	0.78	0.069
Multiparous cows	21.44	7.06	0.66	1.04	0.80	0.33	1.50	0.05	0.48	0.47	0.070
Trial 1 (Faverdin <i>et al.</i> , 1998)	18.92	4.20	0.78	1.17	0.89	-0.14	1.47	0.01	0.37	0.62	0.078
Trial 2 (Faverdin <i>et al.</i> , 2002)	19.30	2.83	0.84	0.96	0.91	0.20	1.11	0.03	0.24	0.73	0.058
Weeks 1–7	17.68	2.95	0.85	1.11	0.90	-0.33	1.29	0.07	0.20	0.73	0.073
Weeks 8–15	20.29	5.01	0.74	1.06	0.85	0.29	1.39	0.04	0.38	0.57	0.068
Milk Production (kg d ⁻¹)											
2 trials	30.52	10.17	0.71	3.26	0.71	-2.05	4.35	0.22	0.22	0.56	0.143
Primiparous cows	26.14	16.17	0.44	2.83	0.26	-3.36	4.87	0.48	0.19	0.33	0.186
Multiparous cows	34.90	10.00	0.73	3.48	0.51	-0.74	3.77	0.04	0.12	0.84	0.108
Trial 1 (Faverdin <i>et al.</i> , 1998)	31.73	10.64	0.72	3.34	0.75	-2.61	4.76	0.30	0.21	0.49	0.150
Trial 2 (Faverdin <i>et al.</i> , 2002)	28.70	11.47	0.63	2.78	0.62	-1.21	3.66	0.11	0.33	0.56	0.128
Weeks 1–7	30.48	10.45	0.75	3.84	0.69	-3.69	5.64	0.43	0.11	0.46	0.185
Weeks 8–15	30.55	8.03	0.75	2.21	0.83	-0.61	2.78	0.05	0.33	0.62	0.091
Complete lactation (Friggens <i>et al.</i> , 1998)											
Total DM intake (kg d ⁻¹)											
All treatments	20.03	0.04	0.98	0.96	0.89	0.36	1.02	0.12	0.00	0.88	0.051
Sequence HH*	27.51	-3.88	1.14	0.97	0.98	0.02	1.27	0.00	0.44	0.56	0.046
Sequence HL*	26.28	-2.04	1.09	1.35	0.97	-0.26	1.48	0.03	0.17	0.80	0.056
Sequence LH*	22.80	3.52	0.83	2.31	0.71	0.43	2.43	0.03	0.09	0.88	0.106
Sequence LL*	21.13	-0.99	1.00	1.71	0.87	1.00	1.96	0.26	0.00	0.74	0.093
Milk Production (kg d ⁻¹)											
All treatments	28.82	-5.64	1.19	2.22	0.87	0.24	2.39	0.01	0.14	0.85	0.083
Sequence HH*	33.21	-2.22	1.10	0.81	0.98	-0.92	1.29	0.50	0.13	0.37	0.039
Sequence HL*	30.77	-7.31	1.24	1.27	0.98	-0.07	1.95	0.00	0.60	0.40	0.064
Sequence LH*	26.20	17.87	0.31	3.02	0.03	0.93	3.32	0.08	0.14	0.78	0.127
Sequence LL*	25.12	-3.01	1.08	2.38	0.42	0.99	2.52	0.15	0.00	0.84	0.100

*HH, High-High; HL, High-Low; LH, Low-High; LL, Low-Low successions of diet net energy concentrations during lactation (see Figure 10).

improvement is required for milk production prediction in early lactation.

Conclusion

This new model is able to simultaneously predict intake and milk production, using only information easily available in practice, and could be useful for many other models or decision support systems in which the prediction of milk production needs to be sensitive to feeding management. It is based on a combination of 'pull forces' attributed to the homeorhesis (Bauman and Currie, 1980) and the 'push forces' of nutrients attributed to the feeding conditions. It represents a good

compromise between simplicity and performance. Some assumptions have been made for combining the marginal responses to protein and energy supplies because of a lack of concept for the milk response to protein and energy interaction. These assumptions can be reconsidered as new results become available, but it appears sufficient, as a first approach, to simulate the differences observed both in intake and milk production owing to diet composition. The first external validations with indoor feeding trials give an idea of the model's ability to simulate a broad range of situations. The model simulations show a good accuracy for the prediction of dry matter intake. The model is also accurate for milk production in mid and late lactation, but could be

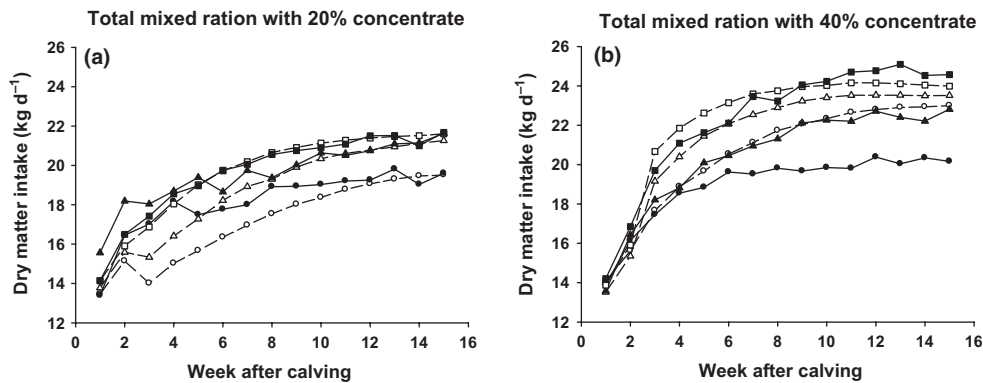


Figure 8 Effect of diet concentrate and protein content on observed (black symbols and solid lines) and predicted (open symbols and dashed lines) voluntary dry matter intake of maize silage-based total mixed ration (adapted from Faverdin *et al.*, 1998). The low (20%, figure a) and high (40%, figure b) concentrate diets were given with low (85 g PDI UFL⁻¹, circle), medium (100 g PDI UFL⁻¹, triangle) or high (115 g PDI UFL⁻¹, square) protein content.

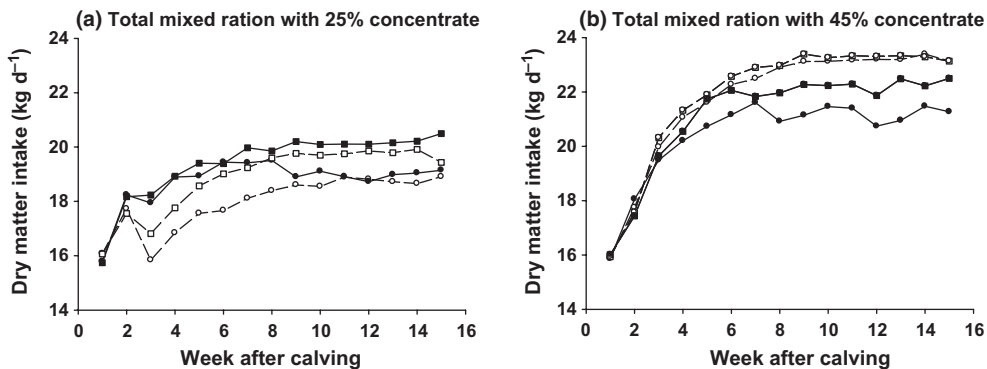


Figure 9 Effect of diet concentrate and protein content on observed (black symbols and solid lines) and predicted (open symbols and dashed lines) voluntary dry matter intake of grass silage and hay-based total mixed ration (adapted from Faverdin *et al.*, 2002). The low (25%, figure a) and high (45%, figure b) concentrate diets were given with medium (92 g PDI UFL⁻¹, circle) or high (110 g PDI UFL⁻¹, square) protein content.

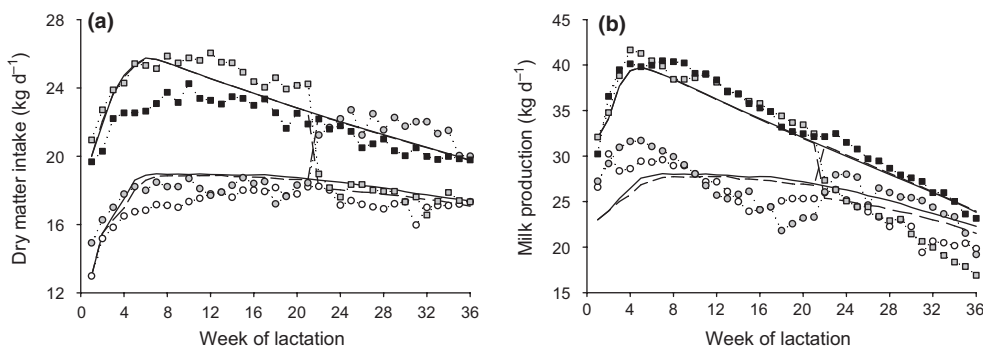


Figure 10 Validation of predicted dry matter intake (a) and predicted milk production (b) during complete lactation with two different types of complete diet High (H) and Low (L) energy concentration (Frignens *et al.*, 1998). These two diets were offered in early (before week 21) or late lactation to four groups with four different sequences: H-H (black square), H-L (grey square), L-H (grey circle), L-L (white circle). The simulated data are plotted in solid lines (H-H and L-L) and dashed lines (H-L and L-H).

improved in early lactation, probably through better prediction of the role of mobilization of body reserves. This model was, however, designed to be also able to predict intake and milk production all year long with all types of diet. The following articles (Delagarde et al., 2011a; 2011b) detail the adaptations of this model to grazing and present some internal and external validations with data obtained in grazing conditions.

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Appendix I

Microsoft® Excel function used to calculate the potential milk production of a dairy cow for a given day of lactation (DIM: day in milk) according to its parity (Parity: primiparous = 1, multiparous = 2), to the production of milk at the peak (MPMax) and to the day of fertilizing insemination (DinsF).

Public Function *pMP* (MPMax, Parity, DIM, DinsF)

Function of the potential milk of a cow according to the stage of lactation and management, the parity and the maximum milk production

```

t = 0
dt = 0.05
VM = 0.155
kg = 0.0305
kH2 = 0.2
CU = 1000
If Parity = 1 Then
    C0 = 2500
    H0 = 0.5
    kH = 0.08
    ks = 0.0015
    pg = 0.02
Else
    C0 = 3000
    H0 = 0.8
    kH = 0.13
    ks = 0.0025
    pg = 0.04
End If
Secretory_cells = C0
Do While t < DIM
    t = t + dt
    HL = H0 × Exp(−kH × t)
    Cell_differentiation = (VM × CU × HL) / (kH2 + HL)
    Cell_death = Secretory_cells × (ks + pg × Exp(−kg × (270 − t + DinsF)))
    Secretory_cells = Secretory_cells + (cell_differentiation − cell_death) × dt
Loop
pMP = Secretory_cells × (2.2 × MPMax + 0.44) / 10000
End Function

```