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Mathematical Modeling of Lactation Curves: A Review of Parametric Models

Mahdi Bouallegue and Naceur M'Hamdi

Abstract

The mathematical representation of milk production against time represents one of the most successful applications of mathematical modeling in agriculture. Models provide summary information, which is useful in making management and breeding decisions. Several empirical mathematical functions have been proposed to describe the lactation curve of dairy cattle differing in mathematical properties, in the number of parameters and in their degree of relationships with the main features of a typical lactation pattern, such as peak yield, time at peak and persistency. This review gives an overview of the parametric models used to fit of lactation curves in dairy cattle. Parametric models are those that found large application to fit the lactation curves, basically due to their limited mathematical complexity, and their abilities to fit a large kind of curves. Models to describe the lactation curve have been classified into two main groups: linear and nonlinear models. Nonlinear parametric functions have represented the preferred tools for modeling lactation curves with the main aim of predicting yields and parameters describing the shape of the curve in addition to important parameters such as peak yield and persistency. Nonlinear models need iterative techniques to be solved. Different iterative methods frequently employed in nonlinear regression models are Marquardt, Newton, Gauss and Dud. Wood model was the most popular parametric model with the largest application can be found in the immediate and easy understanding of relationships between its parameters and main curvatures of the lactation pattern.

Keywords: mathematical modeling, parametric models, nonlinear regression, goodness of fit, shape of lactation curve

1. Introduction

The lactation curves provide useful information for selection programs and for developing suitable management decisions and production strategies at the farm level. So, the modeling of the lactation curve is not a new research topic, the first reference of a model of lactation curve is attributed to Brody et al. [1]. Because of computational difficulties, and the limitations of computer means, early models of lactation curves based on simple logarithmic transformations of exponentials, polynomials, and other linear functions were developed [2]. Mathematical models are able to predict milk yields. The application of these models on the first lactations data can provide important predictive information. Indeed, predicting the evolution

of milk production at the individual or herd level is a powerful tool for managing herd performance. Linear and nonlinear methods were used to estimate the parameters of production peak and inclining and declining phases of milk production during lactation [3]. The incomplete gamma function or Wood function proved relatively powerful in fitting the observed daily milk yield [4]. According to Wood [5], knowledge of the parameters of lactation curves can predict total production from a single control, regarding the number of controls available for prediction. In recent years lactation curve fitting functions have been implemented in dairy farm management software [6]. Moreover, lactation curve modeling is a tool for monitoring individual yields, feeding planning, early detection of diseases before clinical signs appear, and selecting animals for breeding [7]. Another frequently advanced interest in curve production modeling is the measure of persistency. The selection of animals with higher persistency (low decrease of production during the second phase of lactation) is interesting. Thus, cows showing higher yield at the peak of production followed by rapid decline are undesirable and will be easily detected and identified using the adjusted lactation curve. The cost of milk production depends largely on the lactation persistency. The unexpected drop in production after the peak increases the cost of production, because of production inequitably along the lactation [8]. Economically, cows with flat lactation curves are more persistent and produce milk at lower cost [9]. Indeed, the incidence of metabolic and reproductive disorders, arising from the physiological stress of high milk production, would be lowered. The animal may have a more stable diet, favoring in particular the proportion of fodder in the ration and thus reducing production costs [8]. Thanks to these interests and utilities of the lactation curve, the choice of one or more appropriate mathematical functions capable of effectively describing the evolution of milk production throughout lactation is a crucial point. Thus, the interest of the study of the lactation curve is reflected by a multiplicity of mathematical models. Really, the mathematical representation of milk production during the lactation period is one of the most successful applications of mathematical modeling in agriculture [10]. The choice of a model as well as the quantity and the quality of the information necessary for its estimation must, therefore, be reasoned according to the desired use. For example, for studies of the effect of environmental factors on the shape of the lactation curve and the estimation of the classical parameters of the curve by adjusting the data sets classified by groups of animals according to a well-defined factor, a simple model with fewer parameters can meet these objectives. The selection of a mathematical function must, therefore, be based on the ease of parameter estimation, its versatility (possible modeling of the different constituents of the milk and not just the quantity of milk), and the quality of the adjustment. Guo and Swalve [11] recommend the use of the model with the lowest possible number of parameters. The availability of data collected through individual lactation and the development of genetic evaluation methods based on elementary controls, as well as the evolution of the specific requirements of the dairy cattle industry, have oriented the interest of modelers toward more linear functions flexible and general, such as polynomials or splines [12].

2. Description of the standard lactation curve

Milk production evolves during lactation following a cycle that is similar in all dairy females and usually characterized by two different phases: an ascending phase from parturition to peak production (the maximum production) and a downward phase, from this peak to the dry period. The slope of this phase represents the persistency of lactation [13]. Knight and Wilde [14] explain that this phenomenon

is related to the exponential increase in the volume of secretory cells, during gestation due to the phenomenon of hyperplasia (proliferation of cells) and between calving and the peak of lactation by hypertrophy (intensification of their activity). The descending phase of lactation is the longest during which the milk secretion gradually decreases until dry up. This second phase is explained by the involution of secretory cells but especially by the fall of their numbers. The phenotypic expression of these biological processes is represented by standard or typical form (**Figure 1**) of the lactation curve, obtained by plotting on the abscissa the time elapsed since calving and on the ordinate the corresponding daily production [15, 16].

The general appearance of this curve is relatively constant between many domestic species. The lactation curve can be characterized by a number of parameters [13]:

The length of lactation defined by the subscale interval. In most studies concerning lactation curve modeling, this duration is standardized at an interval of 5–305 days. Animals with lactation times greater than 305 days are considered lactations of 305 days [12]. Currently in most countries, several cows have prolonged lactations beyond 305 days.

Total production obtained by combining daily milk production. Total milk yield is considered to be of high economic importance [18]. Total production is also the area under the lactation curve, which mathematically translates as the integral of a mathematical function over the interval of lactation duration.

Initial production (y 0) estimated by the average of the productions of the 4th, 5th, and 6th postpartum days [13].

The growth rate in the ascending phase. This phase ranges from calving to maximum production. Masselin et al. [13] expresses the growth rate of the increasing phase by the difference between the maximum (ym) and the initial production (y0).

The maximum daily production (ym) and the date at which this maximum (tp) is observed.

The peak of production is the highest yield of lactation, and its date is expressed in week (Wood, 1967) or in day. When a mathematical model of adjustment of the lactation curve is available, parameters y_m and t_p are obtained, respectively, as ordinate and abscissa of the point where the derivative of the function of adjustment of the curve $\left(\frac{dy\,(t)}{dt}\right)$ is equal to 0.

The persistency of production in decreasing phase. It is most often identified with a measure of decay of production in a period of time. It is defined as the ability of a cow to maintain milk production after the peak. Assuming uniform nutrition and
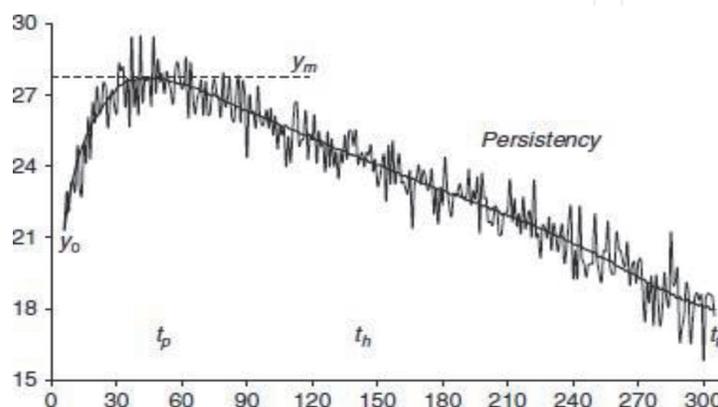

Figure 1.
Lactation curve for dairy cattle (observed and adjusted yields) [17]. With y0 = initial yield; ym = yield at the peak of production; tp = peak time; th = time of mid-lactation; and tf = time of end of lactation.

management conditions, the post-peak decline rate is calculated as the proportion of the decline in milk yield from the previous month, usually ranging from 4 to 9% [14].

3. Mathematical modeling of lactation curve

The interest of the lactation curve is reflected by a variety of mathematical models proposed to describe or predict it. These models are appreciated and used because they have a simple biological or economic interpretation [19].

3.1 Empirical models

An empirical model has a theory that refers only to the level of reality for which the phenomenon being considered is expressed. These so-called empirical models (models based exclusively on experience and observation and not on theory), whether linear or not linear, represent the huge majority of studies published in the bibliography [12]. In fact, empirical models have found great application in different fields of animal science, mainly because of their limited mathematical complexity. Most of them permit to estimate certain classic characteristics of the curve (date and level of the peak of production, persistency, and total production). Many empirical mathematical functions have been proposed to describe the lactation curve of dairy cattle [16, 20]. These functions differ in their mathematical properties, the number of parameters, and their degree of relationship to the main characteristics of a typical lactation structure, such as yield at peak time, persistency, and total yield. Nonlinear parametric models have been a preferred tool for modeling mean curves of homogeneous animal groups [12].

3.2 Parametric curves

To describe the temporal evolution of milk secretion (lactation curve), scientists generally use parametric curves where the variation over time is modeled using linear or nonlinear functions. Most of the mathematical functions proposed to fit lactation curves in dairy cattle are primarily aimed at describing the phenomenon of milk secretion. Their basic assumption is that lactation is characterized by a continuous and deterministic component with an increasing phase to a maximum, followed by a decreasing slope [12]. The mathematical tool used in this approach can be represented by an analytic function of general time:

$$Y = f(t) + \varepsilon \qquad (1)$$

where Y is often the daily output obtained on the day of control t; $f(t)$ is a continuous function, differentiable over the interval represented by the duration of lactation; and ε is the random residual.

The use of parametric models has several advantages. Indeed, these models allow algebraically to calculate characteristic parameters of the curve. For example, the yield and the date of the peak of production are obtained, respectively, as ordinate and abscissa of the point where the first derivative of the function $\left(\frac{df(t)}{dt}\right)$ is equal to 0.

Production between two dates is obtained by calculating the integral of $f(t)$ over this time interval. The total production also corresponds to the integral of the lactation curve over the duration of the lactation.

Another advantage of parametric models is that they summarize distribution characteristics through a small number of parameters (in the majority of cases, three parameters). Rekaya et al. [21] highlighted that a function with a minimum number of parameters and a significant biological interpretation is the most desirable. Although increasing the number of parameters in the model improves the quality of fit for some functions, interpreting the parameters of the most complex models is difficult, and, in many cases, it is impossible to connect them with the classic characteristics of the lactation curve [13].

3.3 Exponential functions

Among the parametric models, lactation curves adjusted by exponential functions or integrating an exponential component into the model formula were widely used. The first attempt to develop a mathematical model to describe the lactation curve dates back to 1923. Brody et al. [1] used an exponential function in the following form:

$$Y_t = a \exp(-ct) \tag{2}$$

This model has been adjusted to monthly lactation yields. Its expression highlights the scaling factor for adjusting production to initial level a and the c parameter associated with the descending phase of the lactation curve and highlighted as a measure of persistency. Although this model is a good attempt to describe the descending phase of the lactation curve, it does not model the growth rate in the ascending phase to reach the peak of lactation. In order to overcome this limitation, Brody et al. [22] presented an improved version of their model, which takes into account the increase in milk yield until production maximum by incorporating an exponential decline function into the model:

$$Y_t = a \exp(-bt) - a \exp(-ct) \tag{3}$$

While this is a great improvement over the first model, Cobby and Le Du [23] reported that this model underestimates milk yield in the middle of lactation and overestimates milk yield at the end of lactation. This model was followed by an exponential parabolic function introduced by Sikka [24] for modeling milk yield:

$$Y_t = a \exp(bt - ct^2) \tag{4}$$

This model provided a good fit for lactation curves of primiparous cows, but it was less effective for multiparous cows, resulting in a bell-shaped curve that does not respect the regularity of the lactation curve around peak production. Then, numerous proposals were made to improve these aspects. Fischer [25] attempted to improve model 3 by replacing the exponential decline integrated in this model by means of a linear decline:

$$Y_t = a - bt - a \exp(-ct) \tag{5}$$

This model underestimated the maximum milk yield and also resulted in a relatively early estimate of the peak date [26]. The individuality of this model is that the ratio a/b estimates the duration of lactation. Vujicic and Bacic [27] attempted to modify model 2:

$$Y_t = t \, c^{-a} \exp(-ct) \tag{6}$$

This model seems to be the first attempt to develop a model that varies both directly and exponentially over time. The disadvantage of this model is that it does not consider the initial evolution to the peak of production. Since the abovementioned exponential models do not correctly translate the ascendant phase of the lactation curve, Wood [28] proposed to adjust the entire curve by an incomplete gamma-type function:

$$Y_t = at^b \exp\left(-ct\right) \tag{7}$$

The incomplete gamma function is probably the most popular parametric model of the lactation curve. It generates the standard form of the lactation curve as the product of a constant, a power function, and an exponential decline function [12]. The disjunction of the Wood equation in its components emphasizes the direct relation of its parameters with the main elements of the shape of the lactation curve. In this expression, the power function t^b permits to integrate the ascending phase of the lactation curve, whereas the exponential term accounts for the downward phase. For these reasons, Wood [28] interpreted parameters b and c as indices of growth intensity and output decline, respectively; the function $t^b \exp(-ct)$ thus appears as the form factor of the curve [13]. Parameter a is then the scale factor of the level of production, which Wood [28] associates with the average production level of the beginning of lactation. Wood [29] tried to justify the use of model 7 from a physiological point of view, but does not interpret parameters b and c from a practical biological point of view. Parameter b is an index of a cow's capacity for the relevant use of energy to produce milk, but mathematically according to Wood [29], parameter b represents the rate of growth of production to yield maximal, and parameter c alternatively represents the rate of decline after the peak of lactation. Cobby and Le Du [23] argued that these interpretations of parameters b and c are fairly simplified and may be erroneous. Wood [30, 31] sought to interpret parameters a, b, and c as a function of the energy flows in the body. According to its approach, the parameter would translate a potential of production which is the function of the intrinsic capacity of secretion of the udder, the level of the mobilizable reserves, and the capacities of ingestion and digestion of the animal. On the other hand, the expression t^b is explained by the fact that all the secretory cells would not be functional immediately after calving. According to Masselin et al. [13], the last aspect should rather be interpreted as the growth of the body's ability to ensure gluconeogenesis to synthesize lactose, which is the main element determining the exit of water from milk. Finally, parameter c would integrate the progressive reduction of the contribution of body reserves to the milk secretion and the exponential decline of the number of secretory cells. Several critics have been reported in Model 7. Cobby and Le Du [23] reported an overestimation of early lactation production and underestimation of peak lactation. Dhanoa [32] reported problems of strong correlations between the estimated parameters. Another reproach has been given to the Wood model that by construction, calving day production is constrained to be zero. This is not real in most mammal species. However, Tozer, and Huffaker [33] have indicated that a cow produces colostrum just after calving, which has no economic value, so considering zero milk yield after calving is not a significant problem. Rowlands et al. [26] reported that the Wood curve does not provide good consistency with the data collected on higher dairy cows at the peak of lactation. According to Macciotta et al. [12], Wood's model limitations are an overestimation of milk production per day in the first part of the curve and an underestimation around and after the peak of lactation. These weaknesses have been reported by some authors [34, 35] primarily because of the multiplicative structure, and the model is characterized by higher correlation between its parameters (ranging from 0.70 to 0.90, [12]) which results in higher sensitivity to data distribution [2].

Despite the limits reported, the Wood model remains the most used function for modeling lactation curves [35]. In addition, it has been used to describe traits other than milk yield, such as fatty acids [37], and it has also been used for adjustment of extended lactations [34, 36]. Many other models have been reported in the literature especially after the appearance of critics of Wood's model. To anticipate these restrictions, many authors have proposed improvements to Wood's model in order to increase its flexibility. As a result, several derivatives of Wood's function have appeared while noting improvements in the modeling of the lactation curve. Beever et al. [20] summarizes the improvements made by these derivatives in greater flexibility in modeling curve shapes and in improving the mathematical properties of the model by decreasing the correlation between model parameters [32]. Cobby and Le Du [23] reported that milk yield after the peak of production declines at a constant rate and proposed a modification of Wood's gamma function, substituting the power function (*tb*) for an asymptotic function of the type exp. (t^b) and replacing the first exponential function of the equation obtained by the function of Gaines resulting in a model of the form:

$$Y_t = a - bt - a \exp(-ct) \tag{8}$$

The advantage of this model over that of Wood [28] is that declines in milk production are modeled exponentially [16]. This model allows a better adjustment of the initial phase of the lactation curve with a good estimate of peak production [26]. Rowlands et al. [26] compared models 3, 7, and 8 and concluded that model 8 describes the initial evolution of milk yield up to 5 weeks better than model 7. They also observed that models 7 and 8 slightly underestimated the initial yield and model 3 slightly overestimated the peak of lactation. Model 7 provided the best position of the peak yield date. According to Olori et al. [38], this model has a parameter that cannot be estimated by linear regression, and this limits its use in practice. Dhanoa [32] proposed a slightly different writing of Wood's model:

$$Y_t = at^{bc} \exp(-ct) \tag{9}$$

Such model reduces the correlations between the parameters of the curve in many cases. In addition, this model provides, with parameter *b*, a direct estimate of the peak lactation date. In an attempt to include a season effect in the Wood model, Goodall [39] proposed the introduction of a categorical variable *D* which takes the value 0 from the period October to March and the value 1 from April to September, resulting in the following model:

$$Y_t = at^b \exp(-ct + dD) \tag{10}$$

where *D* estimates the effect of season. This change takes into account the quantitative estimation of the effect of seasonal changes.

Another modification of Wood's function was attempted by Jenkins and Ferrell [40] (1984) through placing the exponent of *t*, which is the value of *b* in Wood's model equal to 1:

$$Y_t = at \exp(-ct) \tag{11}$$

This model has its limits since curve fitting results have shown that evolution to maximum yield is relatively slow [41]. Based on the model of Cobby and Le Du [23], Wilmink [42] proposed a linear model to describe the lactation curve:

$$Y_t = a + b \, \exp\left(-kt\right) + ct \tag{12}$$

According to Wilmink [42], parameter k is related to the peak of lactation time and usually constitutes a fixed value, derived from a preliminary analysis of average production, implying that the model has only three parameters to estimate. Brotherstone et al. [4] emphasized the importance of parameter k in the ability of the Wilmink model to model daily production in early lactation. In an attempt to overcome underestimation of peak yield and overestimation of yield in the decreasing phase of lactation that results from the use of the Wood model, Cappio-Borlino et al. [43] proposed a nonlinear modification of the Wood model in the following form:

$$Y_t = a \, t^{b \, \exp\left(-ct\right)} \tag{13}$$

while this proposal is more complex than Wood's equation, this model reduces the extent of underestimation at the beginning of lactation and overestimation at the final stage of lactation. Franci et al. [44] have successfully used to adjust the lactation curves of dairy ewes, characterized by a rapid increase in milk yield to the peak of lactation.

4. Linear adjustment models

Dairy production can be considered as a linear combination of the time since calving [13]. Gaines [18] developed a simple linear first-degree model to measure the persistency:

$$Y_t = a - bt \tag{14}$$

In this model, parameter a is an estimator of initial production, and b was proposed as a direct measure of absolute persistency and assumed to be constant during lactation. This model has been compared to other proposals [45], and it has been used to compare feeding strategies of dairy cows with their performance [46].

After the application of this simple linear model, several researchers have attempted to adapt the parabolic or quadratic model whose general form is as follows:

$$y_t = a + bt + ct^2 \tag{15}$$

Dave [47] used a quadratic form for modeling the lactation curve of water buffalo in first lactations:

$$y_t = a + bt - ct^2 \tag{16}$$

Sauvant and Fehr [48] sought to adjust lactation curves of dairy goats by a third-degree polynomial:

$$y_t = a + bt + ct^2 + dt^3 \tag{17}$$

In this model, the interest of the presence of the term of degree 3 with respect to the parabolic model is the introduction of an asymmetry in the curve. The limits of this model are at the level of its parameters b, c, and d which have no biological or zootechnical sense [13]. Dag et al. [49] reported that the cubic model best matched

the data collected in Awassi ewes and allowed for an appropriate description of the shape of the lactation curve. These authors also indicated that the total milk yield estimated by the cubic model was similar to that obtained by the Fleischmann method.

Other higher-degree polynomials have been used to model milk production. With these models, the parameters remain simple to estimate. However, interpretation and biological significance remain a major difficulty. In addition, the adjustments obtained by some authors are satisfactory, but as indicated by Masselin et al. [13], they cover a portion of the lactation curve. Nelder [50] suggested that if biological responses over time were to be modeled with quadratic regression, then it was better to first perform an inverse data transformation. However, a polynomial of the second order is unbounded and tends to be symmetrical with respect to its stationary point, while the characteristic lactation curve is not symmetrical with respect to the asymptote. To obtain an asymmetry, it will be necessary to estimate more parameters. An inverse quadratic polynomial is bounded and generally non-negative and has no integrated symmetry. As a result of these suggestions, Nelder [50] proposed a polynomial function (called the inverse function) to adjust the response curves in multifactorial experiments, particularly in the context of modeling lactation curves. Day t production is described as follows:

$$Y_t = t/a + bt + ct^2 \qquad (18)$$

Yadav et al. [51] were the first to value this design to model the lactation curve of dairy cattle and found it appropriate. According to Batra [52], this model gave a good fit for low-yielding lactations with an early lactation peak. Based on the coefficient R^2, the same author observed that the function 18 gives a better fit than the gamma function when weekly milk control data were used. This function was also greater to parabolic and exponential Wood models for modeling average lactation curves using weekly data from Hariana cows [53]. Olori et al. [38] showed that model 18 underestimates the milk yield around the peak and overestimates it immediately afterwards. An inverse transformation of data as proposed by Nelder [50] to obtain the properties will allow to model the lactation curve with a quadratic polynomial. Singh and Gopal [54] increased the number of parameters by including the term *Log (t)* as an additional co-variable. The introduction of the logarithm breaks the symmetry of the parabolic model [13]. Therefore, these authors have proposed two new models: linear cum log model:

$$Y_t = a - bt + c\,Log(t) \qquad (19)$$

and quadratic cum log model:

$$Y_t = a + bt + c\,t^2 + d\,Log(t) \qquad (20)$$

These authors indicated that these models were superior to the Wood models and the inverse polynomial when fitted to the bi-weekly controlled performance data. At the same time as one of the limits, these models are undefined at *t = 0*, because *Log (t) = ∞* [16], although these models have not been widely applied. They have contributed as support for the development of other models. Ali and Schaeffer [55] added the term *e (Log(t))²* to the second model of Singh and Gopal [54] and proposed the use of a five-variable linear model:

$$y_t = a + bX + cX^2 + f \log(1/X) + e(\log(1/X))^2 \qquad (21)$$

where $X = t$ / *length of lactation*, a is a parameter associated with the peak of production, and f and e are associated with the upward part of the production curve and b and c with the descending part.

Linear model has a greater number of coefficients that allow the adjustment of large forms, while its parameters do not have a technical and biological meaning [12]. Two mathematical models (Ali and Schaeffer and Wilmink) have been used successfully to adjust individual curves [2, 56]. Both models have also been implemented in earlier versions of random regression models [57–59]. A potential problem is raised by the author authors of model 21, and it is that the parameters of the regression model are strongly correlated, which can strongly limit its use. However, the results reported in several studies using this model are contradictory. According to Jamrozik et al. [60], this model gives results very similar to those obtained with the Wilmink model, despite the fact that the Ali and Schaeffer model includes additional parameters. Guo and Swalve [11, 61] have found that this model is less efficient than others, notably that of Wilmink. Concerning the limits of this model, Macciotta et al. [56] found very strong correlations in absolute values (from 0.85 to 0.99) of lactation curve coefficients with a standard form [62]. The correlations obtained by these authors are much higher than those reported by Ali and Schaeffer [55]. Olori et al. [38] compared different functions and showed that the function of Ali and Schaeffer was slightly better than that of Wilmink. Quinn et al. [63] reported that this model is inappropriate for the description of milk component lactation curve (percentages of fat and protein). Schaeffer and Dekkers [64] proposed to adjust the lactation curves by a logarithmic model:

$$Y_t = a + b \log\left(305/t\right) + ct \tag{22}$$

Guo and Swalve [11] introduced the mixed logarithmic model:

$$y_t = a + bt^{1/2} + c\ log\left(t\right) \tag{23}$$

This model can be considered as inspired by model 19 suggested by Singh and Gopal [54], substituting time t for the square root of t in the second term of the model. However, this model tends to underestimate peak yield, while overestimating post-peak yield [38]. Catillo et al. [65] reported that this model was effective in estimating lactation curves and milk production characteristics of Italian water buffaloes.

5. Other models

For a competitive model, Papajcsik and Bodero [66] have introduced trigonometric functions and combined functions with increasing variation such as t^b, $1 - \exp\left(-t\right)$, $Log(t)$, and $\arctan\left(t\right)$ and decreasing functions such as, and, where *arc-tan* and *cosh*, respectively, refer to the *arc-tangent* trigonometric function and the hyperbolic cosine function. These reflections gave birth to the following six models:

$$Y_t = at^b / \cosh\left(ct\right) \tag{24}$$

$$Y_t = a(1 - \exp\left(-bt\right)/ \cosh\left(ct\right) \tag{25}$$

$$Y_t = a \arctan\left(bt\right)/ \cosh\left(ct\right) \tag{26}$$

$$Y_t = a \, Log(bt) \exp(-ct) \tag{27}$$

$$Y_t = a \, Log(bt) / \cosh(ct) \tag{28}$$

$$Y_t = a \arctan(bt) \exp(-ct) \tag{29}$$

The authors compared the effectiveness of 20 different mathematical models, including these six models, and concluded that model 24 and the Wood model better fit the data of the Holstein cows. Although, this study is cited in most of the following studies as an advantage for Wood's function over the model proposed, but we note that this work directs the thinking of modelers to the possibility of the use of complex mathematical models and particularly of trigonometric mathematical functions. An approach was introduced by Grossman and Koops [67] who proposed that lactation could be visualized as a multiphase biological process, that is, visualizing lactation as a two-step process divided in a slant until the peak of lactation is established as the first phase and the progressive decrease in production after the peak as a second phase. The suggested multiphasic logistic function determines the total milk yield by obtaining the sum of the yield resulting from each phase of lactation:

$$Y_t = \sum_{i=1}^{n} \left\{ a_i b_i \left[1 - \tanh^2(b_i(t - c_i)) \right] \right\} \tag{30}$$

where n is the number of lactation phases considered and *tanh* is the hyperbolic tangent function. For each phase i, the maximum yield is equal to ai and bi and occurs at time ci. The duration of each phase is associated with $2b_i^{-1}$ which represents the time required to obtain 75% of the total asymptotic production during this phase. This model has been applied in two-phase or three-phase model, with better adjustment resulting from the three-phase model with a low correlation between residues. For a two-phase model, the first phase could be considered the peak phase because of its proximity to the general spike and its short duration. Likewise, the second phase must be studied because it corresponds to the phase of "persistency." This model has been criticized by Rook et al. [68] who reported lack of justification for lactation to be visualized as a multiphase process. Despite the wide range of models available to adjust lactation curves, the situation cannot be considered satisfactory because of the importance of the remarks that can be made to most of the proposed models. In this regard, an almost general reproach of the comparison of the adjustment quality of these models is the insufficiency of the evaluation of the adjustment's quality. Indeed, the coefficient of determination, which is only a very partial element of this evaluation, is one of the main parameters used for this purpose. Recent studies incorporate residue variation, and the diversification of the results in this respect according to the data used prevents the publication of standard criteria for comparing the quality of the residues of fit models. Olori et al. [38] adjusted data from a single, uniformly managed herd to five mathematical models. They concluded that the relevance of the empirical models of the lactation curve does not depend on the mathematical form of function but on the biological nature of lactation. We notice that the adjusted character remains in most cases the raw milk production. So, it seemed logical to compare the quality of the models for the quantitative level of production.

5.1 Methods applied for adjusting the lactation curve

Nonlinear and linear estimation methods have been used to adjust lactation curves, where the method employed is determined by the nature of the model to be

used. Some models can be developed using a nonlinear and linear estimation at the same time, such as the polynomial regression model of Ali and Schaeffer [55]. Others can be transformed into linear models. Wood [28] has already noted that the gamma function can be converted into a simple linear regression model by performing a logarithmic transformation to determine the initial values of the parameters *a*, *b*, and *c* by means of a least square's estimation. Congleton and Everett [69] reported that the adjustment of the incomplete gamma function with linear regression after a logarithmic transformation has the advantage of requiring a minimum of computational machine time. Due to the large number of lactations analyzed, parameter estimation is obtained by linear regression rather than an iterative nonlinear technique. In linear models the parameters are linear functions of the lactation day, and the least square estimates of the parameters can always be obtained analytically by a simple linear regression. On the other hand, nonlinear models such as the Wilmink function can only be solved by numerical methods following iterative optimization procedures. Adjusting data with a nonlinear regression model has specific advantages. Indeed, nonlinear models are often derived on the basis of biological and/or physical considerations. Thus, the parameters of a nonlinear model usually have direct interpretation in terms of the processes studied. In addition, the main advantage of nonlinear regression compared to other curve fitting procedures is the wide range of functions that can be adjusted. The objective in nonlinear regression is to obtain estimates of the parameters that minimize the residual effects, measured as the sum of the squares of the distances of the data points on the curve [17].

To estimate the parameters following an iterative procedure, it is necessary to have those initial values, which will be subjected to successive iterations. These initial values are adjusted, and the sum of the squares of the residues is reduced significantly to each iteration. The process of estimating the parameters continues until a convergence criterion is met, accepting that from this point on, a negligible or no improvement in data fit is possible [17]. A major difficulty of this procedure is to enter the initial values of the model parameters. If the pre-estimates are not correct, the process may not converge to the minimum of the sum of error squares. Moreover, it is not always possible to know if the process converges toward the best estimate of the minimum of the sum of error squares [70]. The initial values should be reasonably close to the estimates of parameters that are still unknown if the optimization procedure cannot converge. The consequence of a bad choice of the initial parameters is the obtaining of low values of the coefficient of determination, the standard errors that are high [71], and consequently a poor quality of adjustment of the model to data. Fadel [71] discussed a technique for identifying appropriate estimates of initial parameter values using the nonlinear procedure of the statistical analysis system (SAS, PROC NLIN). This technique was illustrated via a segmented nonlinear model with four parameters to estimate (*b1*, *b2*, *b3*, and *b4*), frequently used for the modeling of fiber digestion as a function of fermentation time (*t*):

$$\begin{cases} f_1(t) = b1 + b4, \, si \, t \le b3 \\ f_2(t) = b1 \exp\left[-b2\left(t\text{-}b3\right)\right] + b4, \, si \, t > b3 \end{cases} \tag{31}$$

The principle of this technique consists in using a network of values for *b3* (example of 2 to 6 per unit of 0.1) with fixed estimates of the parameters *b1*, *b2*, and *b4*. The SAS program generates a set of data sets for each proposed value. Then *b1*, *b2*, and *b4* will be calculated for each estimate of *b3* of the proposed network. The combination of the parameters estimated from the solution with the smallest value of the sum of the squares of the residuals will be used as initial values for the final analysis [71].

Different iterative methods such as Marquardt, Gauss-Newton, and Does not Use Derivatives (DUD) are frequently used in nonlinear regression models. The simplest method, known as the DUD, does not require the specification of the partial derivatives with respect to the parameters of the mathematical model. It is an algorithm that brings the derivatives closer by differences. However, it is important to note that this algorithm does not give good estimates especially when the parameters are strongly correlated. Another method commonly used in nonlinear regression is the iterative Gauss-Newton method also available in SAS. The algorithm of this technique is based on Taylor series development near the initial parameter values [67]. Generally, Marquardt's nonlinear regression was the most commonly used method to adjust lactation curves using nonlinear models [34]. The Marquardt method, which follows an intermediate path between the Gauss-Newton (Taylor series method) and Newton (second derivative) methods, was often considered better to achieve convergence when the parameter estimates were strongly correlated [34].

6. Lactation curve of milk constituents

Lactation curves relating milk yield and milk constituents would be considered for influencing different of lactation curves. However, it is necessary to consider factors that influence milk yield and milk constituents, for example, different genetic, effect of climate, and nutrition. These factors will cause changes in milk compositions and milk yield which may be the data for prediction of the lactation curve and lactation persistency [72]. This link has already been studied at the phenotypic and genetic level. The genetic correlations of milk yield with negative percent of fat and protein were negative (0.25 and 0.27, respectively), and the same sign was observed at the phenotypic level (0.28 and 0.39, respectively) [72]. The ordinary description of milk secretion refers to the appearance of changes in milk composition during lactation, i.e., the decrease in milk yield is accompanied by an increase in fat and protein contents. Milk composition can be used as a diagnostic and monitoring tool in nutritional assessment [73]. Several studies have shown a correlation between energy levels and milk composition using different traits such
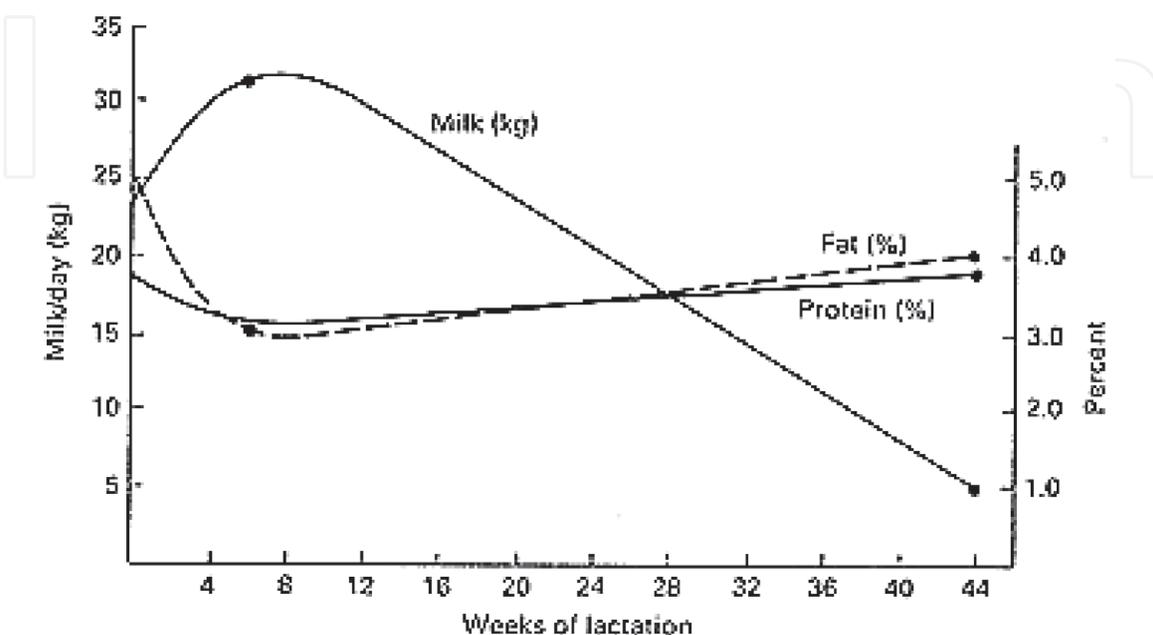

Figure 2.
Lactation curves for milk production, percent fat, and percent milk protein (Wood, 1976).

as fat/protein ratio (FPR), protein/fat ratio, fat/lactose ratio [74]. Higher FPR values are associated with a decrease in dry matter intake and an increase in fat mobilization on the negative energy balance phase after calving [73]. Thus, FPR changes in milk may be an indication of a cow's ability to adapt to the requirements of milk production and postpartum reproductive efficiency [75]. The richness of the milk (fat and protein contents) follows an inverse curve to that of the milk secretion, mainly because of the effect of the dilution. It decreases rapidly during the first weeks, stabilizes at a minimal level (nadir point), and rises again due to less dilution. The relative composition of milk constituents changes profoundly during the first days after parturition. The concentration of immunoglobulins decreases rapidly after parturition in favor of caseins. The nadir point of the fat concentration curve is reached approximately 3 weeks after peak lactation of milk yield, while that of protein is established near the peak of lactation [15]. As a result, milk fat and protein are often modeled with the same functions as those used to model milk production, provided that they can take a convex form. Most of the models generated for the description of the lactation curve focused only on milk yield, although the first reference found on the adjustment of lactation curve adapted to milk composition was that of Wood [28] who studied its seasonal variation. **Figure 2** illustrates the shape of the lactation curve of milk yield and its fat and protein composition, expressed as a percentage and adjusted by the incomplete gamma function of Wood.

7. Conclusion

Mathematical models allow the lactation curve to be represented in terms of a set of parameters to be estimated. Various models have been used to study the lactation in dairy cattle. Each function has advantages and disadvantages. Parametric models such as Wood and Wilmink models have several advantages. Indeed, parametric models offer the possibility to calculate primary and secondary parameters, which have a biological meaning and are therefore easy to interpret. These parameters are key elements to study the effect of the environment factors on the shape of the lactation curves. Recently the increased availability of records per individual lactations and the genetic evaluation based on test day records has oriented the interest of modelers toward general linear functions, as polynomials or splines. But these functions present some computational difficulties especially at the level of the lactation curves parameters.

Author details

Mahdi Bouallegue[1]* and Naceur M'Hamdi[2]

1 Higher Institute of Agronomy of Chott-Meriem, Sousse, Tunisia

2 National Agronomic Institute of Tunisia, Tunis, Tunisia

*Address all correspondence to: mahdibouallegue@yahoo.fr

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