Model Selection for Nondestructive Quantification of Fruit Growth in Pepper

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ABSTRACT. Quantifying fruit growth can be desirable for several purposes (e.g., prediction of fruit yield and size, or for the use in crop simulation models). The goal of this article was to determine the best sigmoid function to describe fruit growth of pepper (*Capsicum annuum*) from nondestructive fruit growth measurements. The Richards, Gompertz, logistic, and beta growth functions were tested. Fruit growth of sweet pepper was measured nondestructively in an experiment with three different average daily temperatures (18, 21, and 24 °C) and in an experiment with six cultivars with different fruit sizes (20 to 205 g fresh weight). Measurements of fruit length and fruit diameter or circumference were performed twice per week. From these, fruit volume was estimated. A linear relationship related fruit fresh weight to estimated fruit volume, and a Ricker or polynomial function related fruit dry matter content to fruit age. These relations were used to convert estimated fruit volume into fruit fresh and dry weights. As dry weight increased until harvest, fitting the sigmoid function to the dry weight data was less suitable: it would create uncertainty in the estimated asymptote. Therefore, the sigmoid functions were fitted to fresh weight growth of the fruit. The Richards function was the best function in each data set, closely followed by the Gompertz function. The fruit dry weight growth is obtained by multiplication of the sigmoid function and the function relating fruit dry matter content to fruit age.

In many cases, it is desirable to quantify the growth of horticultural products with functions (e.g., to analyze growth differences between treatments or as an input for crop simulation models). In all cases, measurements of fruit growth and quantification of the growth over time are needed.

Measurement of fruit growth can be done destructively, by regularly harvesting fruit (Arena and Curvetto, 2008; Hubbard and Pharr, 1992; Nielsen et al., 1991), and nondestructively, by performing repeated measurements on dimensions of fruit still attached to the plant (Garriz et al., 2005; Godoy et al., 2008; Greer, 2005; Pagamas and Nawata, 2008). Both methods have their advantages and disadvantages: repeated nondestructive measurements on the same fruit allows for following the growth of individual fruit and for investigation of variation in growth between fruit. On the other hand, repeatedly touching the fruit

to measure them might also disturb their growth. Destructive harvest enables direct measurements of fruit weight (fresh or dry); with nondestructive measurements, intermediate equations are needed to convert fruit dimensions into fruit fresh or dry weight (e.g., Cuevas et al., 2003; De Silva et al., 1997; Marcelis, 1992; Marcelis and Baan Hofman-Eijer, 1995).

After obtaining the measurements, either destructively or nondestructively, the best equation describing the growth of the fruit needs to be selected. Growth of fruit like tomato (*Lycopersicon esculentum*) and sweet pepper follows a sigmoid growth curve (Adams et al., 2001; Marcelis and Baan Hofman-Eijer, 1995). The logistic, Gompertz, and Richards functions are often used to describe fruit growth over time (Adams et al., 2001; Barrera et al., 2008; Cuevas et al., 2003; Daymond and Hadley, 2008; Garriz et al., 2005; Marcelis, 1992; Tadesse et al., 2002). However, these functions have different properties with respect to their shapes. Comparison of different sigmoid functions and model selection should be done to assure the most appropriate one is used.

For different types of fruit and developmental rates, this article aimed at obtaining growth functions for growth of individual fruit of pepper. We tested which of the most commonly used functions, namely the logistic, Gompertz, and Richards functions, was most suitable to describe fruit growth of *Capsicum*. We also applied the beta growth function (Yin et al., 2003). The goal was to describe

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growth as the increase in weight, so attention is paid to the intermediate functions by which the fruit dimensions can be related to fruit weight. As both the growth in fresh weight and the growth in dry weight were obtained, the question is answered whether it is more appropriate to fit the sigmoid function to fresh fruit weight or dry fruit weight. Two experiments were used, one in which one cultivar was grown at three different average daily temperatures and one with six different cultivars with varying fruit sizes.

Materials and Methods

Experiments

Fruit growth curves of pepper were obtained in two experiments. The first experiment considered fruit of one cultivar growing at three temperatures (18, 21, and 24 °C), while in the second experiment, fruit growth was measured on six different cultivars (Medina, Fireflame, Furila, Gepetto, Nazar, and Funky).

TEMPERATURE EXPERIMENT. The experiment was conducted in air-conditioned compartments (2.5 × 5.4 m) of a Venlo-type glasshouse in Wageningen, The Netherlands, with *C. annuum* cv. Mazurka (RijkZwaan, De Lier, The Netherlands). Three compartments were used, in which the average temperature was set at 18, 21, or 24 °C. There was a difference of four degrees between day and night temperatures. Day temperature was from 0800 to 1800 HR, and night temperature was from 2000 to 0600 HR, and the hours in-between were used for heating up and cooling down. The realized daily average temperatures were (mean ± SD): 18.3 ± 0.5, 20.3 ± 0.35, and 23.3 ± 0.31 °C. Vapor pressure deficit was kept constant at 0.7 kPa, resulting in average relative humidities of 67%, 73%, and 77% at 18, 21, and 23 °C, respectively. Plants were grown in 15 L pots with one plant per pot, filled with commercial peat-based potting medium (Lentse potgrond nr 4; Horticoop, Katwijk, The Netherlands), and plant density was 4.7 plants/m². Water was given daily, while fertilization with a standard nutrient solution [12N–6.1P–19.9K+2Mg (PG-mix; Yara Benelux, Vlaardingen, The Netherlands)] was given once or twice per week, the latter later in the growth period. The experiment was performed from March until July 2007. The average daily global outside radiation was (mean ± SD) 15.5 ± 2.9 MJ·m⁻²·d⁻¹.

CULTIVAR EXPERIMENT. The experiment used six *C. annuum* cultivars that produce fruit of different fresh weights [as given by De Ruiter Seeds (Monsanto Vegetable Seeds), Bergschenhoek, The Netherlands]. ‘Medina’ (20 g), ‘Fireflame’ (20 g), and ‘Furila’ (45 g) were hot pepper cultivars, and ‘Gepetto’ (135 g) was a sweet pepper cultivar with pointed fruit. ‘Nazar’ (140 g) and ‘Funky’ (205 g) produced block-type sweet peppers. Plants were grown in a Venlo-type glasshouse compartment (12 × 12.8 m) on rockwool substrate in Wageningen, The Netherlands, in a randomized complete block design, from April until Sept. 2007 at a density of 3.8 plants/m². Average temperature was (mean ± SD) 21.6 ± 2.0 °C, and average daily global outside radiation was 16.3 ± 5.6 MJ·m⁻²·d⁻¹.

Measurements

The method used to derive fruit dry weight growth was similar to the one described by Marcelis and Baan Hofman-Eijer (1995). Half of the plants in each experiment were used to obtain fruit growth curves. The other half of the plants in the experiments were used for observations on fruit abortion, fruit set, and plant growth (see Wubs et al., 2009, 2011). In

both experiments, plants used to obtain fruit growth curves were divided into three groups, to perform three types of measurements.

In the first group of fruit, fruit dimensions were repeatedly nondestructively measured. Flowers were tagged at anthesis, and their anthesis date was denoted. To minimize variation in fruit size, plants were pruned to one or two fruit per plant. Other fruit and flowers from those plants were removed, and new flowers were removed weekly. Twice per week, length and diameter (in the cultivar experiment except for cultivar Gepetto) or circumference (in the temperature experiment, and cultivar Gepetto in the cultivar experiment) of the tagged fruit were measured with a caliper or tape measure. Diameter or circumference was measured in the middle of the fruit. The measurements were done between anthesis and harvest of the fruit. The age of the fruit (time after anthesis) at every measurement time was known for these fruit. Fruit were harvested when completely red, which was beyond the stage when fruit are commercially harvested (75% red). Fresh and dry weights of the harvested fruit were measured. Dry weight was measured by drying the fruit in the oven for 48 h at 105 °C. Number of nondestructively measured fruit differed between the treatments (Table 1). Fewer plants were available in the temperature experiment than in the cultivar experiment. The treatment 24 °C in the temperature experiment and the cultivar ‘Gepetto’ in the cultivar experiment had fewer measured fruit because of their vulnerability to blossom-end rot (BER). Fruit with BER were not included in the analyses.

A second group of fruit was harvested at different fruit sizes. Their fruit dimensions (length and diameter or circumference) were measured as described above, and their fresh weight was also measured. These measurements were used to obtain a relationship between fruit fresh weight and fruit volume.

In the last group of fruit, flowers were tagged at anthesis and harvested at various fruit ages. Fresh and dry weights of these fruit were measured. Dry weight of fruit was obtained by drying the fruit in the oven for 48 h at 105 °C. These measurements were used to obtain a relationship between fruit dry matter content and fruit age.

Selecting flowers for measurements of fruit growth curves started about 2 weeks after the first flowers appeared. Other fruit were selected and harvested randomly during the experiment.

Table 1. Number of nondestructively measured fruit (*N*) and average fruit growth duration of pepper fruit in the temperature and cultivar experiments.

Expt.	Treatment	<i>N</i>	Fruit growth duration	
			(d)	(°Cd)
Temperature	18 °C	17	88 c ^z	737
	21 °C	23	76 b	789
	24 °C	6	64 a	873
Cultivar	Medina	83	55 a	
	Fireflame	70	57 b	
	Furila	51	59 c	
	Gepetto	29	66 d	
	Nazar	53	66 d	
	Funky	33	69 e	

^zDifferent letters within an experiment indicate significant differences between treatment levels with Tukey test, *P* ≤ 0.001 for both experiments.

Intermediate calculations and functions

Fruit volume V was calculated for all fruit on which fruit dimensions were measured from length l and diameter d as $V = \frac{1}{4}\pi l d^2$ or from length l and circumference c as $V = \frac{1}{4\pi} l c^2$, assuming a cylindrical fruit shape.

From the measurements on the second group of fruit, a relationship between fruit fresh weight and fruit volume was established. For pepper fruit, a linear relationship was appropriate (Marcelis and Baan Hofman-Eijer, 1995). Relationships were fitted per experiment. No intercept was fitted, and tests for the difference in slopes between treatment levels were conducted ($\alpha = 0.05$).

For the temperature experiment, the ages of the fruit were converted into degree-days, assuming a base temperature of 10 °C (Marcelis et al., 2006). The ages of the fruit in the cultivar experiment were scaled between 0 and 1, with anthesis as 0 and the actual fruit growth duration when harvested mature (red), or to the average fruit growth duration (Table 1) when harvested before maturity, as 1.

Fruit dry matter content of a pepper fruit measured in the third group of fruit was calculated as its dry weight divided by its fresh weight (grams dry weight/grams fresh weight). Fruit dry matter content was arcsine-square-root transformed before analysis to normalize the data (Sokal and Rohlf, 1995). The data of the temperature experiment were complemented with the data on fruit dry matter content and fruit age from Marcelis and Baan Hofman-Eijer (1995), which were obtained at 20 °C. Measurements from the third group of fruit were used to establish a relationship between fruit dry matter content and fruit age. Three functions were fitted to the data of fruit dry matter content (fdm) vs. fruit age t : a Ricker function (Eq. [1]; Bolker, 2008), the sum of the exponential functions Eq. [2], and a third- or fourth-order polynomial. For simplicity, the nontransformed fruit dry matter content in Eqs. [1] and [2] is given as the dependent variable.

$$\text{fdm} = c_R - a_R(t - d_R)\exp(-b_R(t - d_R)), \quad [1]$$

$$\text{fdm} = a_s \exp(b_s t) + c_s \exp(d_s t), \quad [2]$$

where t is the age of the fruit (time after anthesis). The Ricker function Eq. [1] has an asymptote c_R . Parameters b_R and d_R determine the position of the minimum. In the sum of two exponentials, a_s and c_s determine the value at $t = 0$, and b_s and d_s are the relative growth rates. Polynomial functions were fitted with linear regression, while the other two functions were fitted with nonlinear regression. As the spreading of the data from the different treatment levels over the time axis was not equal, testing for differences between treatment levels resulted in differences that were due to this unequal division of data points rather than differences between the treatments. One fit was therefore done to all treatment levels of the temperature experiment. For the cultivar experiment, the fit is only done for the cultivars Nazar and Funky, for which sufficient data over the total growth period were gathered.

The calculated fruit volumes of the repeatedly nondestructively measured fruit were converted into fruit fresh weight, using the relation between fruit fresh weight and calculated fruit volume. Subsequently, fruit fresh weight was converted into fruit dry weight with the function relating fruit dry matter content to fruit age. Under- or overestimations of the final calculated dry weight were corrected to the measured dry weight by the ratio

(measured dry weight/calculated dry weight). This ratio was applied to the full growth curve of the particular fruit (i.e., at all measurement times).

Statistical analysis

Four functions describing sigmoid growth were fitted to the measurements of nondestructive fruit growth: Richards function Eq. [3], logistic function Eq. [4], Gompertz function Eq. [5], and beta growth function Eq. [6]. These functions are able to describe fruit growth in time with one mathematical formula, and the parameters of the functions are easily interpretable.

$$w(t) = \frac{w_{\max}}{(1 + v e^{-k(t-t_m)})^{1/v}}, \quad [3]$$

$$w(t) = \frac{w_{\max}}{(1 + e^{-k(t-t_m)})}, \quad [4]$$

$$w(t) = w_{\max} e^{-e^{-k(t-t_m)}}, \quad [5]$$

$$w(t) = w_{\max} \left(1 + \frac{t_e - t}{t_e - t_m} \right) \left(\frac{t}{t_e} \right)^{\frac{t_e}{t_e - t_m}}, \quad [6]$$

where $w(t)$ is the fruit weight at time t (time after anthesis), $w_{\max}$ is the upper asymptote, k is a constant determining the curvature of the growth pattern, and t_m is the position of the inflection point, where the growth rate is maximum. In the Richards function, v is a shape parameter, and t_e in the beta growth function indicates the end of the growth period. The logistic function is the Richards function when $v = 1$, and is symmetric around t_m . The Gompertz function equals the Richards function in case $v = 0$. In contrast to the other functions, in the beta function, weight at $t = 0$ is exactly zero and the function has exactly the value $w_{\max}$ at time t_e . The constraint $w_t = w_{\max}$ when $t > t_e$ was set, to get an upper asymptote. The Gompertz, Richards, and beta growth functions are able to describe asymmetric functions around t_m .

The nondestructive measurements of fruit growth took place on individual fruit, resulting in numerous individual growth curves. This made the fitting process different from destructive measurements, where the measurement points would be independent. Averaging all measured growth curves to one growth curve per treatment would have resulted in loss of information, just as averaging the parameters of individual fits on each fruit would do. Fitting the functions to the fruit weights in time was done with nonlinear mixed modeling. This method takes into account that all measurements of one fruit are dependent on each other and that variance differed between the measurements of different fruit. The method assumes a normal distribution of the parameter values and estimates the average values and standard deviations for the parameters of the fitted function ($w_{\max}$, k , t_m , etc.). The growth of a specific fruit is described by a set of parameters sampled from these normal distributions for each parameter. The deviation of a parameter of a specific fruit from the mean parameter value is the random effect. The mean and standard deviation of each parameter can depend on the treatment level, in this case temperature and cultivar.

As a first step, a function for fruit growth (Eqs. [3]–[6]) was fitted without effect of the treatment on model parameters, but with a random effect for each parameter, plus correlations between the random effects of the parameters. When a trend between random effects and the treatment was observed (e.g., one treatment level having mainly positive random effects, while others having mainly negative effects), the parameter was made dependent on treatment. This process was repeated until the addition of a treatment effect for a parameter did not improve the model further. When the best model with respect to fixed effects was obtained, model improvement continued with checking whether a first-order autocorrelation between the measurements points improved the fit. Furthermore, attention was paid to the random effects: whether the correlations between the random effects were needed, whether a random effect for a certain parameter was needed, and whether the variance associated with the random effect depended on treatment level. Residual variances were made dependent on treatment level if necessary. To test whether a change in the model form improved the fit (e.g., a model with and without correlations between the random effects), log-likelihood tests were performed ($\alpha = 0.05$). In some cases, a newly added parameter of the model made a previous added parameter redundant. The latter parameter was in that case removed from the model. The final model was checked by inspecting the normality of residuals and random effects, as well as trends of the residuals with the fitted values.

Comparing the different functions for the fruit growth, the Akaike information criterion {AIC (Eq. [7])} was used, which takes into account the log-likelihood of the model as well as the number of parameters. Furthermore, the mean deviation {MD (Eq. [8])} and the root mean square error {RMSE (Eq. [9])} between fitted and observed values are

$$\text{AIC} = -2 * \log\text{-likelihood} + 2 * p, \quad [7]$$

$$\text{MD} = \frac{1}{n} \sum_{i=1}^n (P_i - O_i), \quad [8]$$

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2}, \quad [9]$$

where p is the number of parameters in the model, n is the number of data points, P_i is the predicted value of observation i , and O_i is the observed value of observation i .

All fits were done in R 2.12.2 (R development core team, 2011). The nlme package was used for fitting the mixed models (Pinheiro et al., 2011).

Results

Relation between fruit fresh weight and estimated fruit volume

In both experiments, the relationship between fruit fresh weight and estimated fruit volume was well fitted with a linear regression without intercept ($R^2 = 0.99$ for both fits). Slopes were different between treatments in both experiments ($P < 0.001$ for both experiments). At 24 °C, the slope was lower than at 18 and 21 °C, implying a lower fruit fresh weight at the same fruit volume (Table 2). In the cultivar experiment, the slopes for ‘Medina’ and ‘Fireflame’ (hot peppers with similar shape and weight) were not

significantly different ($P = 0.36$), but slopes were different ($P = 0.001$) for ‘Nazar’ and ‘Funky’ (sweet peppers with similar shape but different weights).

Relation between fruit dry matter content and fruit age

There was hardly a difference between the three functions for the relationship between fruit dry matter content and fruit age (fourth-order polynomial, the biexponential function, and the Ricker function) in the temperature experiment (Table 3; Fig. 1). The differences between the two cultivars in the cultivar experiment were minimal (Fig. 2). A third-order polynomial was fitted, which differed only in the first-order term. The Ricker function only differed in the asymptote c , while here was no difference in the biexponential model. In both data sets, the fruit dry matter content seemed to stabilize as the fruit matured (Figs. 1 and 2), but this was beyond the age of the average time of harvest (Table 1). The asymptote fitted in the Ricker function (≈ 0.12 in both experiments) was also higher than the fruit dry matter content at harvest (which was 0.07–0.09 for both experiments). This implies that fruit dry matter increase still continued.

Sigmoid functions

FIT SIGMOID FUNCTIONS ON FRESH OR DRY WEIGHT GROWTH?

The ultimate goal is to obtain a function that describes the dry weight growth of a fruit in relation to its age for different temperatures or cultivars. However, when the measurements of fruit dimensions were converted into fresh and subsequently

Table 2. Slope of relation between fruit fresh weight and estimated fruit volume of pepper fruit in the temperature and cultivar experiment. Slope is given in grams fresh weight per cubic centimeter, and N represents the number of data points in each regression. Values between brackets are the standard errors of the slopes. R^2 was 0.99 for both experiments.

Expt.	Treatment	N	Slope
Temperature	18 °C	196	0.487 (0.003) b ^z
	21 °C	198	0.491 (0.003) b
	24 °C	139	0.407 (0.003) a
Cultivar	Medina	238	0.592 (0.015) e
	Fireflame	186	0.615 (0.020) e
	Furila	178	0.516 (0.008) d
	Gepetto	200	0.348 (0.002) a
	Nazar	342	0.434 (0.002) b
	Funky	288	0.425 (0.002) c

^zDifferent letters within an experiment indicate significant differences between the treatments ($P \leq 0.05$).

Table 3. Akaike information criterion (AIC) for the functions relating fraction dry matter of the pepper fruit to fruit age in the temperature and cultivar experiments. Cultivar experiment refers only to cultivars, Nazar and Funky.

Expt.	Function	AIC
Temperature	Polynomial	–2830
	Biexponential	–2825
	Ricker	–2831
Cultivar	Polynomial	–1594
	Biexponential	–1510
	Ricker	–1548

into dry weight, dry weight showed no clear plateau at the end (Figs. 3 and 4). Volume and fresh weight of the fruit do not change in the last 10 d before harvest (Marcelis and Baan Hofman-Eijer, 1995). Also in the present data, fruit fresh weight showed a sigmoid shape with a clear plateau in the end (Figs. 5 and 6). The slope of the relationship between fruit dry matter content and fruit age did not equal zero at the moment of harvest

Fig. 1. Fruit dry matter content (grams dry weight/grams fresh weight) of pepper fruit as function of fruit age (expressed in degree-days) in the temperature experiment. Symbols represent the measurements, $\diamond$ = 18 °C, $\times$ = 20 °C, $\square$ = 21 °C, and $\triangle$ = 24 °C; the lines represent the fit of specified functions, — = Ricker function, - - - = polynomial function, and - · - = biexponential function.

Fig. 2. Fruit dry matter content (grams dry weight/grams fresh weight) of pepper fruit as function of fruit age (expressed in days) for the six different cultivars. (A) 'Nazar' and (B) 'Funky'. Symbols represent measurements; lines represent fit of specified functions, — = Ricker function, - - - = polynomial function, and - · - = biexponential function.

(Figs. 1 and 2), as explained in the previous paragraph. Therefore, the sigmoid functions were not fitted to estimated dry weight, but to estimated fresh weight.

SIGMOID CURVES FITTED ON FRESH WEIGHT. Fruit growth as a function of temperature sum was nearly similar for the three used temperatures (Fig. 5). The initial increase in fruit fresh weight was slightly lower and the maximum growth rate was reached later at 24 °C than at either 18 or 21 °C. Later maximum growth rate was reflected in differences in parameter t_m between the temperatures (Tables 4 and 5). In all models, a random effect was needed for w_{max} , but not for the other parameters (Tables 4 and 5). The autocorrelation between the measurements was considerable (Table 5). Except for the beta function, all fits had a residual variance, which depended on the temperature. The

Fig. 3. Estimated dry weight growth of pepper fruit in the temperature experiment: (A) 18 °C, (B) 21 °C, and (C) 24 °C. Symbols represent the average over five data points. Lines represent the final fruit growth curve, resulting from the multiplication of Richards function for fruit fresh weight and the Ricker function for the relationship between fruit dry matter content and fruit age. Error bars represent the SE when larger than the symbol.

Fig. 4. Dry weight growth of pepper fruit in the cultivar experiment: (A) 'Nazar' and (B) 'Funky'. Symbols represent the average over five interpolated data points. Lines represent the final fruit growth curve, resulting from the multiplication of Gompertz function for fruit fresh weight and the polynomial function for the relationship between fruit dry matter content and fruit age. Error bars represent the SE when larger than the symbol.

best-fitting model was the Richards function, followed by the Gompertz, logistic, and beta growth functions (Table 6). The logistic and beta growth functions overestimated growth in the first phase of fruit growth (Fig. 5). The growth rate of the Richards function in the first bend of the curve (before the phase of fast growth) is higher than for the Gompertz function.

The fruit growth curves of the six cultivars mainly differed in the final weight (Fig. 6), resulting in difference between the cultivars in the parameter $w_{\max}$ (Tables 4 and 5). Fitting the growth functions revealed that also the growth rate parameter k differed between the cultivars (Tables 4 and 5). In all models, random effects were needed for $w_{\max}$ and t_m ; for $w_{\max}$, the variance differed between the cultivars. Parameter k only had a random effect in the Gompertz and Richards functions. The autocorrelation between the data points in these models was not significant. In all models, the residual variance depended on the cultivar. AIC indicated the Gompertz function as the best function although the MD and RMSE were slightly higher than in the Richards function (Table 6). The negligible difference between the Gompertz and Richards functions was reflected in the value of d , which was close to zero (Table 5). The logistic and beta growth functions fitted less well, as indicated by a higher AIC. These functions overestimated the first part of the fruit growth (Fig. 6). The Gompertz and Richards functions underestimated growth in the first phase for the hot peppers and 'Gepetto', while slightly overestimating growth for the block-shaped sweet peppers 'Nazar' and 'Funky'.

In all models of the two experiments, parameter t_m had a value around one-third of the fruit growth duration, with the logistic and beta growth functions estimating higher t_m values than the Gompertz and Richards functions (Table 5). Parameter t_e in the beta growth function was estimated around two-thirds of the average growth period.

Fig. 5. Estimated fresh weight growth of pepper fruit and fitted functions thereon in the temperature experiment: (A) 18 °C, (B) 21 °C, and (C) 24 °C. Inset magnifies the first 200 °Cd of the graph when necessary. Symbols represent the average over five data points. Error bars represent the SE when larger than the symbol. Lines represent the average growth curve of the different functions. — = Richards function, - - - = Gompertz function, . . . = logistic function, and - · - · = the beta growth function.

Discussion

A question arising in this paper was whether the sigmoid functions had to be fitted to fresh weight growth or to dry weight growth. It turned out that fitting a sigmoid curve to the time course of fruit dry weight was less suitable as a sigmoid shape with a clear plateau was not observed (Figs. 3 and 4). Data from literature also indicate the absence of a clear plateau when dry weight is plotted against time {e.g., for cucumber [*Cucumis sativa* (Marcelis, 1992)], sweet pepper (Barrera et al., 2008), and tomato (Ho et al., 1982/3 [sic])}. Fitting a sigmoid curve to dry weight growth would therefore cause a relatively large uncertainty in the estimation of $w_{\max}$. The parameter $w_{\max}$, the final fruit weight, is an important indicator for fruit quality and is also an important factor in modeling as $w_{\max}$ has a large impact on, for example, dry matter partitioning and fruit abortion. A good fit of $w_{\max}$ is therefore important. Fruit fresh weight often stabilizes before the fruit is harvested (Figs. 5 and 6; Barrera et al., 2008; Nielsen et al., 1991; Turhan et al., 2006). Therefore, the sigmoid curves should be fitted to fresh weight over time. Dry weight over time can be obtained by the product of the

Fig. 6. Estimated fresh weight growth of pepper fruit and fitted functions thereon in the cultivar experiment: (A) 'Medina', (B) 'Fireflame', (C) 'Furila', (D) 'Gepetto', (E) 'Nazar', and (F) 'Funky'. Inset magnifies first 20 d of the graph when necessary. Symbols represent the average over 10 interpolated data points. Error bars represent the SE when larger than the symbol. Lines represent the average growth curve of the different functions. — = Richards function, - - - = Gompertz function, - - - = logistic function, and - · - · = the beta growth function.

sigmoid function for fresh weight and the function describing the relation between fruit dry matter content and fruit age. The result is shown in Figs. 3 and 4. Except for 24 °C in the temperature experiment, the resulting fit properly described the dry weight data.

All tested functions described the fresh weight growth of sweet pepper rather well. In the temperature experiment, the Richards function had the lowest AIC, MD, and RMSE and no strong over- or underestimations and hence had the best fit to the fresh weight against fruit age. It implied that the extra flexibility provided by extra parameter ν was needed, as is often observed (Brown and Mayer, 1988). However, the Gompertz function fitted nearly as well, especially in the cultivar experiment. Fruit growth was clearly not symmetric around the time of fastest growth, and thus the logistic function fitted worse than the Richards and Gompertz functions. The beta growth function was introduced by Yin et al. (2003) and has been successfully used in different crops (Condori et al., 2008; Müller et al., 2006; Vocanson and Jeuffroy, 2008). Here, it fitted less well than the other functions. Parameters t_m and t_c were unaffected by the treatments (Tables 4 and 5), which can be due to the scaling of the growth duration. Variation in growth curves can therefore only be obtained with w_{max} , which was not sufficient to account for the different shapes of the measured growth curves. As a consequence, the number of

parameters in the beta growth function was considerably lower than for the other functions (Table 6).

The temperature levels used in the present experiment hardly influenced fruit weight, implying that a shorter growth period under high temperatures was compensated for by higher growth rates. However, a repetition of the experiment under lower light levels showed a decrease in fruit size with increasing temperature (171, 175, and 139 g fresh weight at 18, 21, and 24 °C, respectively). Assimilate supply was likely to be limiting in that case. The present results are in contrast with cucumber and tomato. In cucumber, fruit fresh weight under nonlimiting assimilate supply increased when temperature increased from 17.5 °C to 20 °C and 25 °C (Marcelis and Baan Hofman-Eijer, 1993). In tomato, fruit fresh weight under nonlimiting assimilate supply decreased when temperature increased from 19 to 23 °C (De Koning, 1994). At 24 °C, most fruit suffered from BER. BER is correlated to high initial fruit growth rate (Marcelis and Ho, 1999). So the fruit from which fruit growth was obtained at 24 °C were the fruit with a somewhat slower fruit growth rate in the initial phase (Fig. 5), and this is reflected by a difference in the parameter t_m (Table 5). Using temperature sum

as a measure for time did not result in similar growth times (expressed in degree-days) for three temperatures (Table 1), as was also the case in tomato (De Koning, 1994).

There were large differences in fruit growth between the cultivars; apart from the obvious difference in final size w_{max} , the growth rate parameter k also differed between cultivars: it was lower for large-fruited cultivars. Parameter t_m did not differ between the cultivars because of scaling of time to the fruit growth duration but would on day basis differ between the cultivars (Barrera et al., 2008).

The relationship between dry matter content of the fruit and fruit age was fitted with three different functions: two of them, the biexponential function and the polynomial function, had no asymptote, whereas the Ricker function had an asymptote c_R . The data indicated an asymptote, but value of the fitted asymptote was higher than the one estimated from the dry matter content of the mature fruit. Apart from temperature and cultivar, the fruit dry matter content can be influenced by fruit load, season, and salinity (De Koning, 1994).

Estimated fruit volume was used to calculate fruit fresh weight. González-Real et al. (2009) fitted a linear relationship between fruit dry weight and estimated fruit volume of sweet pepper. For the present data, such a relationship would have an $R^2 \approx 0.7$, compared with $R^2 = 0.99$ for the relationship between fruit fresh weight and estimated fruit volume. A relationship

Table 4. Dependency of parameters on treatment levels, presence of random effects for each parameter and the autocorrelation between data in the nonlinear mixed model fit of pepper fruit fresh weight growth.

Expt.	Function	Fixed effects dependent on treatment level ^z				Random effects present and dependent on treatment level ^y				Autocorrelation	Residual variance dependent on treatment level ^x
		$w_{\max}$	t_m	k^w	d	$w_{\max}$	t_m	k^w	d		
Temperature	Logistic	–	+	–		+	–	–		0.76	+
	Gompertz	–	+	–		+	–	–		0.73	+
	Beta growth	–	–	–		+	–	–		0.79	–
	Richards	–	+	–	–	+	–	–	–	0.72	+
Cultivar	Logistic	+	–	+		++	+	–		0.28	+
	Gompertz	+	–	+		++	+	+		–	+
	Beta growth	+	–	–		++	+	–		0.46	+
	Richards	+	–	+	–	++	+	+	–	–	+

^z+ means parameter dependent on treatment level; – means parameter not dependent on treatment level.

^y++ means random effect present and depending on treatment level; + means random effect present but not depending on treatment level; – means random effect absent.

^x+ means dependent on treatment level; – means not dependent on treatment level.

^wIn the beta function, column k indicates parameter t_e .

Table 5. Parameter values for the different treatment levels in the temperature and cultivar experiments. Logistic, Gompertz, Richards, and beta growth functions were fitted to fresh weight growth of pepper fruit. For each parameter, mean and standard deviation per treatment level are given.

Expt.	Treatment level	$w_{\max}$ (g fresh wt)								t_m (°Cd/–) ^z							
		Logistic		Gompertz		Richards		Beta		Logistic		Gompertz		Richards		Beta	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Temperature	18 °C	181.9	33.73	185.8	34.57	184.4	34.35	180.8	33.55	303	0	265	0	279	0	344	18.05
	21 °C	181.9	33.73	185.8	34.57	184.4	34.35	180.8	33.55	319	0	282	0	296	0	344	18.05
	24 °C	181.9	33.73	185.8	34.57	184.4	34.35	180.8	33.55	347	0	312	0	326	0	344	18.05
Cultivar	Medina	31.6	5.53	32.4	5.75	32.5	5.76	31.1	5.34	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02
	Fireflame	29.0	5.53	29.6	5.74	29.7	5.75	28.7	5.33	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02
	Furila	61.6	12.61	66.5	13.25	63.6	13.27	60.5	11.97	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02
	Gepetto	139.6	26.81	142.7	28.08	142.9	28.13	142.5	26.65	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02
	Nazar	122.5	20.89	126.9	21.39	127.3	21.40	119.5	19.73	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02
	Funky	198.7	30.00	205.1	30.07	205.6	30.08	194.6	29.38	0.37	0.03	0.32	0.03	0.32	0.03	0.40	0.02

Expt.	Treatment level	k (1/°Cd/–) ^y				t_e (°Cd/–) ^z				v (–)	
		Logistic		Gompertz		Richards		Beta		Richards	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Temperature	18 °C	0.014	0	0.0097	0	0.011	0	544	11.55	0.31	0
	21 °C	0.014	0	0.0097	0	0.011	0	544	11.55	0.31	0
	24 °C	0.014	0	0.0097	0	0.011	0	544	11.55	0.31	0
Cultivar	Medina	13.41	0	8.60	0.96	8.40	0.95	0.61	0	–0.05	0
	Fireflame	14.31	0	9.49	0.96	9.27	0.95	0.61	0	–0.05	0
	Furila	12.28	0	7.97	0.96	7.77	0.95	0.61	0	–0.05	0
	Gepetto	16.45	0	10.82	0.96	10.54	0.95	0.61	0	–0.05	0
	Nazar	11.51	0	7.28	0.96	7.08	0.95	0.61	0	–0.05	0
	Funky	12.31	0	7.84	0.96	7.63	0.95	0.61	0	–0.05	0

^zUnit was °Cd for the temperature experiment and dimensionless for the cultivar experiment because of scaling.

^yUnit was 1/°Cd for the temperature experiment and dimensionless for the cultivar experiment.

between fruit volume and fruit dry weight was not appropriate as fruit with similar volumes can have different fruit dry weights, caused by variation in fruit age (which influences fruit dry matter content), and fruit of the same age can have different fruit volumes because of differences in assimilate supply.

Concluding, this study shows that sigmoid function on fruit weight growth of sweet pepper could better be fitted to fresh weight, and not to dry weight, as fruit dry weight still increased at the time of harvest. To obtain dry weight, the function fitted to fresh weight could be multiplied by the function relating fruit

dry matter content to fruit age to obtain the growth in dry weight (Figs. 3 and 4). The Richards and Gompertz functions are preferred for describing fruit growth of pepper. Temperature did not affect fruit size within the temperature range used but did affect fruit growth duration and fruit growth rate. Cultivar influenced fruit size as well as fruit growth rate. Results are used in the simulation of sweet pepper crop growth (Wubs, 2010) and can be used to make simulation stochastic, by varying parameters for fruit growth between the fruit.

Table 6. Measures of goodness-of-fit and number of parameters for the final fits of four sigmoid curves on fruit fresh weight of pepper in the temperature and cultivar experiments. The mean deviation (MD) and root mean square error (RMSE) are given for the difference between predicted and observed values. Akaike information criterion (AIC) is determined by the number of parameters and the log-likelihood of the model.

Expt.	Function	MD	RMSE	AIC	Parameters (no.)
Temperature	Logistic	0.70	9.33	4773	10
	Gompertz	-1.70	8.90	4749	10
	Beta growth	1.21	10.58	4826	8
	Richards	-0.78	8.70	4738	11
Cultivar	Logistic	0.52	5.33	22001	27
	Gompertz	0.04	4.01	21645	27
	Beta growth	0.63	6.77	22399	22
	Richards	0.01	3.98	21650	28

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