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Fruit Growth Patterns of Four Apple Cultivars Using Nonlinear Growth Models

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Summary

Fruit diameter increase was monitored in four apple cultivars during three consecutive years (2006–2008) from t-stage until harvest. Individual fruit diameter increase was described using a negative exponential equation. Fruit growth curves of early ('Gala Brookfield'), mid-season ('Golden Delicious Reinders') and late ripening apple cultivars ('Braeburn Hillwell', 'Fuji Kiku 8') were denoted with an appropriate nonlinear model and each model parameter was evaluated separately. Apple fruit analyzed in the present study exhibited a similar growth curve for all analyzed cultivars i.e. a linear increase in fruit diameter in the beginning of fruit growth, followed by a slow curvilinear enlargement towards the asymptote in the final stages of fruit growth a few weeks before technological maturity. Asymptote was significantly dependent on cultivar, exhibiting higher correlation between predicted final fruit diameter and measured fruit diameter at harvest for late ripening cultivars. Similar growth rates have been calculated for 'Gala Brookfield', 'Golden Delicious Reinders' and 'Fuji Kiku 8' and a slower growth rate was characteristic for 'Braeburn Hillwell' cultivar.

Key words. diameter increase – growth curves – *Malus domestica* – statistical model

Introduction

Advanced knowledge of apple fruit development from fruitlet to maturity is crucial for optimal prediction of year-to-year yields and fruit quality. Apple (*Malus domestica* Borkh.) fruit growth has been defined as sigmoidal increase in fruit diameter or fresh weight, although several authors describe it as curvilinear in the first stages of expansion followed by a steady linear increase (Lakso et al. 1995). This growth pattern closely resembles physiological development of apple fruit, which can be split into two distinct but interlocked processes; rapid cell division and a later, cell size increase (elongation and enlargement) (Austin et al. 1999). Authors report, that cell division in apple fruit ceases about 5 to 6 weeks after full bloom followed by cell expansion (Al-Hinai and Roper 2004).

Understanding general fruit growth pattern is important for timing of different technological processes in apple orchards. Fruit thinning, pest and disease control management, optimal irrigation and harvest, as well as other practices critically depend on the correct time of implementation (Westwood 2009; Kaack and Pedersen 2011). Moreover, elucidating apple growth curves can help set timestamps for potential fruit size prediction and, consequently yield forecast. The latter is needed for competitive advantages in fresh-market planning as a great yearly fluctuation is common in worldwide apple production (Wulfsohn et al. 2012). Yield forecasting with an input of field-survey or probability-based sampling data combine fruit counts and size measurements with pre-calculated growth curves and correlations between fruit diameter and mass (Wulfsohn et al. 2012; Zhou et al. 2012). The impact of several factors on apple growth curves has been monitored and determined. Among them temperature, long- or short-term water stress, and applied technological practices (thinning, hormone application) have been confirmed to influence apple development (Stern et al. 2003; Kaack and Pedersen 2010).

The competitiveness of apple fruit as a sink is related firstly, to the number of its cells and secondly, the physiological status (Lakso et al. 1995). These are determined not only by environmental factors or cultural practices but are also genetically predisposed. Cultivar, rootstock,

plant age, biennial bearing, the position of the flower on spur potentially affect the final size of apple fruit (Lakso et al. 1995; Ferree et al. 2001; Atay et al. 2010). However, genetic determination of seasonal growth curves has rarely been studied although research focusing on root-stock-graft interactions and final apple size determination or quantification has been published (Al-Hinai and Roper 2004; Karlidag and Esitken 2012).

Growth has been described as an irreversible increase in weight and mass (Atay et al. 2010), and final apple size is pre-determined for specific apple cultivars. Although apple cultivars all bloom within a short but similar time period, mostly dependent on seasonal factors, apple growth and fruit maturation time varies substantially among cultivars. In temperate environments, early cultivars mature 70–90 days after full bloom (DAFB) and late cultivars 150–160 DAFB (Schechter et al. 1993). Differences in genetic and seasonal growth curves for early and late ripening apples have rarely been studied over a period of several years and mathematical models describing their specifics are still lacking.

The present study aims to describe apple fruit growth of early, mid-season and late ripening apple cultivars using an appropriate nonlinear model and draws attention to differences or similarities among cultivars in model parameters. The analysis and growth curve characterization expands through several consecutive years and includes data from the beginning of cell expansion stage onward elucidation the diameter increase of 4 apple cultivars until harvest at technological maturity. Model appropriateness is discussed. The study assesses eventual discrepancies between model-predicted final fruit size and real-time final fruit size of analyzed cultivars. The understanding of specific growth curves of widely planted apple cultivars can help fine tune pruning, fruit thinning, harvest, and the use of fertilizers, growth regulators or irrigation and evaluate yields in commercial orchards.

Materials and Methods

Location and plant material

Apple fruit growth was monitored in an orchard located at the Fruit Growing Center Gacnik near Maribor, NE Slovenia (latitude 46° 33' 17" N, longitude 15° 38' 48" E, altitude 280 m) over 3 consecutive years (2006, 2007, 2008). Climatic conditions were recorded on site during the analyzed years (Table 1). Four apple cultivars were included in the growth pattern study: early to mid-season ripening 'Gala Brookfield' and 'Golden Delicious Reinders', and late-ripening, 'Fuji Kiku 8' and 'Braeburn Hillwell' cultivars all grafted on M9 and trained to a slender spindle. The orchard was planted in 2003 at a density of approximately 3000 trees per hectare. The orchard was equipped with drip irrigation system, covered with black hail nets and managed according to integrated production measures. A crop density of 4–6 fruit per trunk cross-sectional area was ascertained by hand thinning prior to the first measurement at t-stage of fruit development. T-stage has been described as the phase when the underside of the fruit and stalk form the letter T (Blanke and Kunz 2009).

Sampling

Four trees per cultivar were randomly selected and the same trees were monitored each year to ensure equal measuring conditions. On each tree, 12 apples were individually labelled according to the characteristics of the fruiting wood: 1. Terminal bud on one-year-old wood (30–40 cm), 2. Terminal bud on two-year-old wood and, 3. Terminal bud on three-year-old wood. Per fruiting wood, 4 replicates were monitored for each tree at each sampling. Apple fruit growth (apple diameter, mm) was measured nondestructively at regular intervals (5–7 days) at the widest point of the fruit equatorial plane with a dig-

Table 1. Average monthly temperatures, temperature anomaly and total monthly precipitation and precipitation anomaly for collection site in years 2006, 2007 and 2008.

Measurements	Average monthly temperature (°C)			Temperature anomaly			Total monthly precipitation (mm)			Precipitation anomaly (%)		
Year	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
Apr	11.6	13.7	11.0	1.6	3.7	1.0	94	10	39	117	12	49
May	15.2	17.2	15.9	0.6	2.6	1.3	128	134	35	135	142	37
Jun	19.7	21.2	20.2	1.8	3.3	2.3	83	60	96	70	50	81
Jul	23.4	22.4	21.3	3.8	2.8	1.7	54	112	110	46	95	93
Aug	17.8	20.2	20.7	−0.9	1.5	2.0	137	129	134	106	100	105
Sep	17.4	13.9	14.9	2.2	−1.3	−0.3	73	173	61	74	175	62
Oct	12.9	9.5	11.6	2.8	−0.6	1.5	30	71	44	34	82	51

ital calliper. The first measurement was taken at t-stage of fruit development and the monitoring continued until fruit harvest at technological maturity (harvest maturity), when the mass of all sampled apples has also been recorded (Table 2).

Data analysis

Prior the further analysis data of all fruits which did not reach the technological maturity (fell off prematurely) were removed. 14.4 % of data was removed and data of 360 apple fruits was evaluated in forthcoming analyses. The diameter of apple fruits was regarded as a parameter of fruit growth and a response variable and time as independent variable. Time variable for all fruit growth data was normalized to days after full bloom (DAFB).

Individual fruit diameter growth patterns were described using negative exponential model. As show by VON BERTALANFFY (1938) this is theoretically the correct equation to describe isometric growth using one dimensional growth parameters such as fruit diameter. The following equation was used:

$$D(t) = \varphi_1\left(1 - e^{(-e^{\varphi 2}(t-\varphi_3))}\right) \quad \text{[Eq. 1]}$$

D(t) fruit diameter at time t after full bloom
φ1 parameter, describing the asymptote of the curve (potential final fruit size)
φ2 parameter, determining the steepness of the curve (related to growth rate)
φ3 parameter, determining the intersection with the x-axis.

Next, each model parameter was individually compared between cultivars, years and fruiting wood using factorial ANOVA. Assumptions of ANOVA (homoscedasticity and normality) were tested graphically using boxplots and QQ-plots, rather than formally (Levene test, Sahiro-Wilk test) which almost always show significant deviations from normality and homoscedasticity for large sample sizes even when these deviations are trivial (QUINN and KEOUGH 2002). Duncan post-hoc test was used to discriminate between significant factor effects and their interactions. All analyses were performed in R environment (R CORE TEAM 2012). Nonlinear models were fitted using the library nlme.

Results and Discussion

Fruit diameter data collected at defined intervals from t-stage until fruit harvest were combined into a unified model illustrating growth curves for all analyzed cultivars. Of the factors being evaluated fruiting wood had no effect on growth curve parameters so it was excluded from the forthcoming analyses. Growth patterns seem fairly similar among cultivars and years (Fig. 1) and show a negative exponential shape. The parameters of the average model according to the equation 1 across all cultivars, fruiting woods and years are the following (mean estimate and 95 % confidence interval): φ1: 93.5 (92.2 – 94.8), φ2: −4.43 (−4.46 – −4.41) and φ3: 9.2 (8.75 – 9.65). Coefficient of determination (R2) of the average model is 91.3 % and means squared error is 0.997. The pairwise correlations between parameters were lower than 0.65 so we did not regard the model being overparameterized. As checked graphically (not shown here), deviations from normality and homoscedasticity assumptions were minor or lacking which justifies the use of ANOVA. ANOVA was calculated for each parameter separately to evaluate the impact of analyzed factors on general apple growth curve (Table 3). Of three parameters evaluated only parameters φ1 and φ2 are discussed for their biological significance. Parameter φ3 shifts the curve in × direction and is not regarded biologically explainable (otherwise it is related to initial fruit diameter). Predicted final fruit dia-

Table 2. Onset of full bloom, T-stage and harvest maturity, and the number of measurements taken each year for individual apple cultivar.

Cultivar/ Measurements	'Braeburn Hillwell'			'Fuji Kiku 8'			'Gala Brookfield'			'Golden Delicious Reinders'		
Year	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
Full bloom	Apr 26th	Apr 17th	Apr 18th	Apr 28th	Apr 17th	Apr 21st	Apr 27th	Apr 16th	Apr 21st	Apr 30th	Apr 17th	Apr 22nd
T-stage	May 21st	May 7th	May 12th	May 24th	May 10th	May 15th	May 21st	May 7th	May 13th	May 16th	May 11th	May 16th
Harvest maturity	Oct 10th	Sep 26th	Sep 24th	Oct 10th	Sep 26th	Sep 24th	Sep 5th	Aug 16th	Aug 28th	Sep 26th	Sep 12th	Sep 17th
No of sampling dates	21	21	18	21	21	18	16	15	14	19	19	17

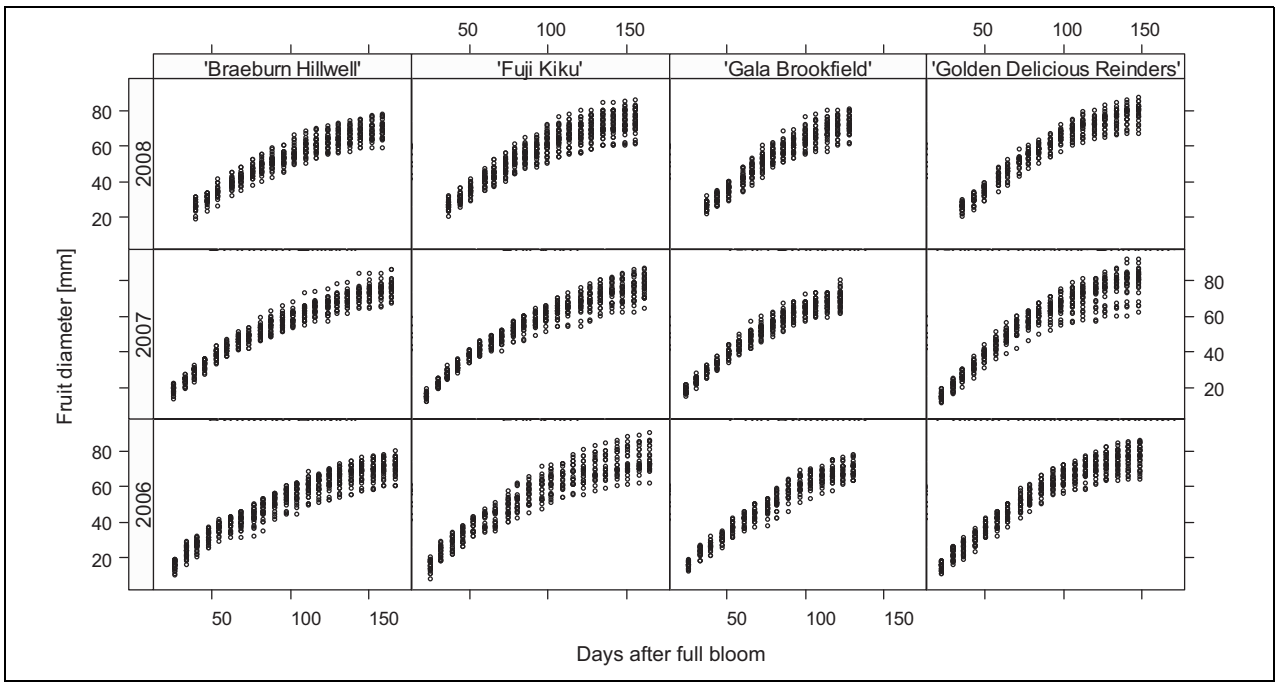


Fig. 1. Growth patterns of 360 investigated apple fruits of four cultivars in three consecutive years.

Table 3. ANOVA table calculated for each parameter and their interactions to predict the impact of analyzed factors on general apple growth curves.

ANOVA	φ1			φ2			φ3		
	df	F value	P-value	df	F value	P-value	df	F value	P-value
Cultivar	3	9.428	0.000	3	9.969	0.000	3	44.631	0.000
Year	2	1.422	0.243	2	8.689	0.000	2	35.65	0.000
Position	2	0.155	0.856	2	0.362	0.697	2	7.548	0.063
Cultivar:year	6	2.338	0.032	6	1.74	0.111	6	2.698	0.014
Cultivar:position	6	1.085	0.371	6	0.809	0.563	6	0.317	0.928
Year:position	4	0.307	0.873	4	0.901	0.464	4	1.732	0.143
Cultivar:year:position	12	1.284	0.226	12	2.054	0.020	12	1.148	0.320

meter (parameter φ1) was significantly dependent on cultivar and a weak cultivar:year interaction has also been confirmed (Fig. 2). This suggests that the final model-predicted fruit diameter (described by the asymptote of the curve) is genetically controlled and is affected to a moderate extent by other internal and external analyzed factors. Interestingly, the asymptote for early-ripening cultivar 'Gala Brookfield' and mid-season ripening 'Golden Delicious Reinders' was determined significantly higher compared to late-ripening 'Fuji Kiku 8' and 'Braeburn Hillwell'. The theoretical model-predicted final fruit diameter for early ripening cultivars differs greatly from fruit diameter at technological maturity reported by different authors (Atay et al. 2010; Ozkan et al. 2012). It can be speculated that early-ripening cultivars reach technological maturity relatively early in their development and their growth would continue beyond the technological maturity. It is generally known that 'Gala' strains in particular vary significantly in final fruit diameter over years being greatly dependent on temperatures, location and other environmental factors (Warrington et al. 1999). Additionally, it is computationally difficult to estimate the asymptote of fruit growth where the growth stops by early technological maturity; in some years (e.g. 2006 for 'Gala Brookfield') the growth seems almost linear (Fig. 1). On the other hand, the model-predicted asymptote (parameter φ1) for late-ripening 'Fuji Kiku 8' and 'Braeburn Hillwell' better fits the diameter at harvest reported by Talaie et al. (2011). Also, R2 for 'Fuji Kiku 8' apples describing the correlation between predicted

	φ1			φ2			φ3		
ANOVA	df	F value	P-value	df	F value	P-value	df	F value	P-value
Cultivar	3	9.503	0.000	3	9.434	0.000	3	43.909	0.000
Year	2	1.333	0.265	2	8.839	0.000	2	32.969	0.000
Cultivar:year	6	2.336	0.032	6	1.684	0.124	6	2.671	0.015

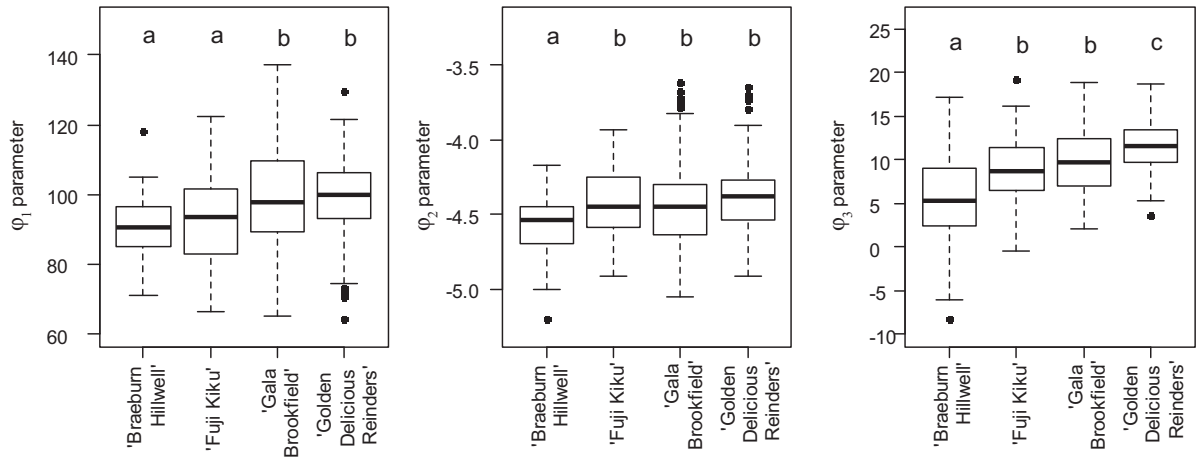


Fig. 2. ANOVA results and homogeneous groups for cultivar factor of individual model parameter describing apple fruit growth.

upper asymptote and observed (measured) fruit diameter was significantly higher compared to other cultivars (Fig. 3).

However, the inherent growth potential, or specifically the prospective final fruit diameter of selected cultivars described by the growth asymptote (parameter φ1) has to be distinguished from actual final growth. Namely, model predictions always describe growth under optimal conditions but in reality limited resources and competition from other sinks determine final apple fruit diameter (Lakso et al. 1995). Modeling approaches, elucidating apple fruit growth, thus report complex connections among external factors influencing final harvest size (Welte 1990; Lakso et al. 1995) but all agree on the major importance of internal i.e. genetic limitations to diameter increase similarly to the present model. The difference between asymptote and actual final diameter is larger for early ripening cultivars.

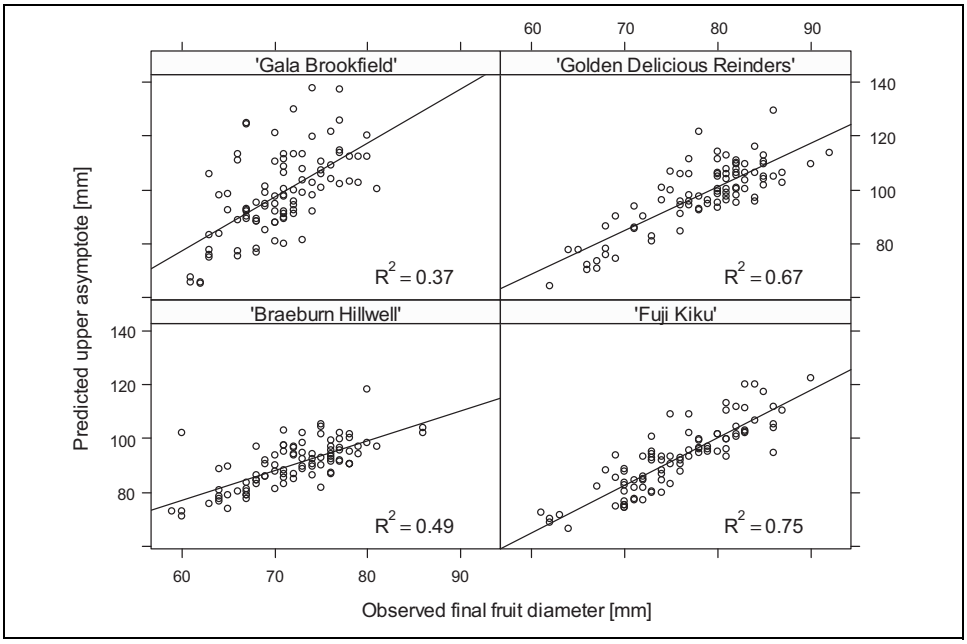


Fig. 3. Relationship between observed final apple fruit diameter and upper asymptote predicted on the basis of diameter growth data of individual apple fruits of four investigated cultivars.

Parameter φ2, determining the slope of the curve, shows the growth rate of the analyzed cultivars (Fig. 2). Again, the differences have been confirmed for cultivar and year, but no interaction has been determined. Similar growth rates have been calculated for 'Gala Brookfield', 'Golden Delicious Reinders' and 'Fuji Kiku 8'. A slower growth rate was characteristic for late-ripening 'Braeburn Hillwell' cultivar. A similar time-dependent diameter change (growth rate) has been demonstrated in a study of Atay et al. (2010) who compared 'Galaxy Gala' and 'Braeburn' cultivar. The latter demonstrated a different growth dynamics to that of early-ripening cultivars.

The modeled growth pattern describes the diameter increase of analyzed cultivars following the exponential cell division phase, which is reportedly curvilinear (Lakso et al. 1995). Namely, during the first 3–6 weeks apple size increase is largely a result of cell number multiplication and the fruit growth is slow (Lakso et al. 1995; Al-Hinai and Roper 2004). After t-stage (physiologically and practically dividing the two distinct growth phases) the increase in apple fruit diameter can predominately be ascribed to vacuolization of cells, individual cell size increase and rapid development of intercellular spaces (Warrington et al. 1999) and approximately linear growth pattern has been reported (Atay et al. 2010). This has also been confirmed by Goudriaan and Monteith (1990) who linked the linear increase with constant light interception after tree canopy closure. Apple development in the second (cell expansion) phase is thus primarily uniform but a late-season decline in fruit diameter increase has also been detected (Lakso et al. 1995). Apple fruit analyzed in the present study exhibited a similar growth curve (diameter increase) for all evaluated cultivars (Fig. 1). Firstly, it demonstrated a linear increase in fruit diameter followed by a slow curvilinear enlargement towards the asymptote. All cultivars are thus characterized by a slow growth rate in the final stages of fruit growth a few weeks before technological maturity. However, in 'Gala Brookfield' the linear diameter increase was extended until only several days prior to harvest.

Growth curve shape of biological data strongly depends on growth measure being evaluated. As shown by von Bertalanffy (1938) organism length follows negative exponential curve which has its mechanistic background. Fruit diameter is, similarly as an organism length, 1-dimensional measure of size so von Bertalanffy's model can be applicable also to fruit diameter growth data. This model describes the growth well when growth is isomorphic (no temporal change of shape) which holds for the apple fruit quite well too. In some papers such negative exponential curve shapes of fruit diameter growth were used (Warrington et al. 1999; Austin et al. 1999) although sometimes different (inappropriate) equations were also used to describe this measure of growth (Garriz et al. 1999).

As discussed previously, growth is a three-dimensional increase of an object so when studying growth of apple fruits the volume or fresh weight are often measured (Schechter et al. 1993; Lakso et al. 1995; Chakespari et al. 2010). The problem of this approach, however, is the destructiveness of the measurements which precludes the monitoring of the same fruits through time. To overcome this problem the diameter or weight might be estimated using known diameter-volume or diameter-weight relationships (De Silva et al. 1997; Warrington et al. 1999). By definition, the relationship between apple fruit diameter and volume/weight is third-order polynomial. Because the most appropriate growth model should follow mechanistic rules, for volumetric growth such a model can be obtained by combining equation 1 with the equation of the sphere:

$$V(t) = \frac{\pi}{6}\varphi_1^3 \left(1 - e^{(-e^{\varphi 2}(t-\varphi_3))}\right)^3 \quad \text{[Eq. 2]}$$

and for weight growth simply multiplying the equation 2 with apple fruit density ($\rho \approx 0.75–0.85$ g cm^{-3}):

$$W(t) = \rho\frac{\pi}{6}\varphi_1^3 \left(1 - e^{(-e^{\varphi 2}(t-\varphi_3))}\right)^3 \quad \text{[Eq. 3]}$$

Additionally, a correction factor can be added for asphericity of the apple fruit and for density changes during fruit growth. This, however, does not change the general curve shape of all analyzed cultivars which is asymmetric sigmoidal (Fig. 4). This specific model type has rarely been applied to apple fruit growth so far. Purely empirical expolinear (Lakso et al. 1995) or even (segmented) linear (Schechter et al. 1993) models were rather used. These predict constant fruit growth till maturity and no decrease in growth rate (upper asymptote) and describe fruit growth well for a given narrower period of growth. Upper asymptote of weight or volume is rarely traceable since fruits reach their maturity beforehand especially early ripening apple varieties, such as 'Gala Brookfield', in our case.

Divergence of real data from predicted values of models after equations 1, 2 and 3 is possible also due to suboptimal environmental conditions. Presence of drought, heat, pests, nutrient limitation, suboptimal light conditions, excessive fruit load can strongly affect fruit growth resulting in unusual growth curves (e.g. double sigmoidal).

It can, however, be concluded that a negative exponential growth pattern is universal for apple cultivars growing in typical circumstances. A linear increase in fruit diameter in the beginning of fruit growth is followed by a somewhat slower enlargement in the final stages of fruit growth. Interestingly, early ripening cultivars, such as 'Gala Brookfield' analyzed in the study, are characterized by a relatively linear increase of fruit diameter up until harvest. Theoretically, early-ripening cultivars reach technological maturity relatively quickly and their growth could continue beyond that set time-stamp. Slight differences in growth patterns of early- and late-ripening cultivars during fruit development should be considered for optimal apple orchard management.

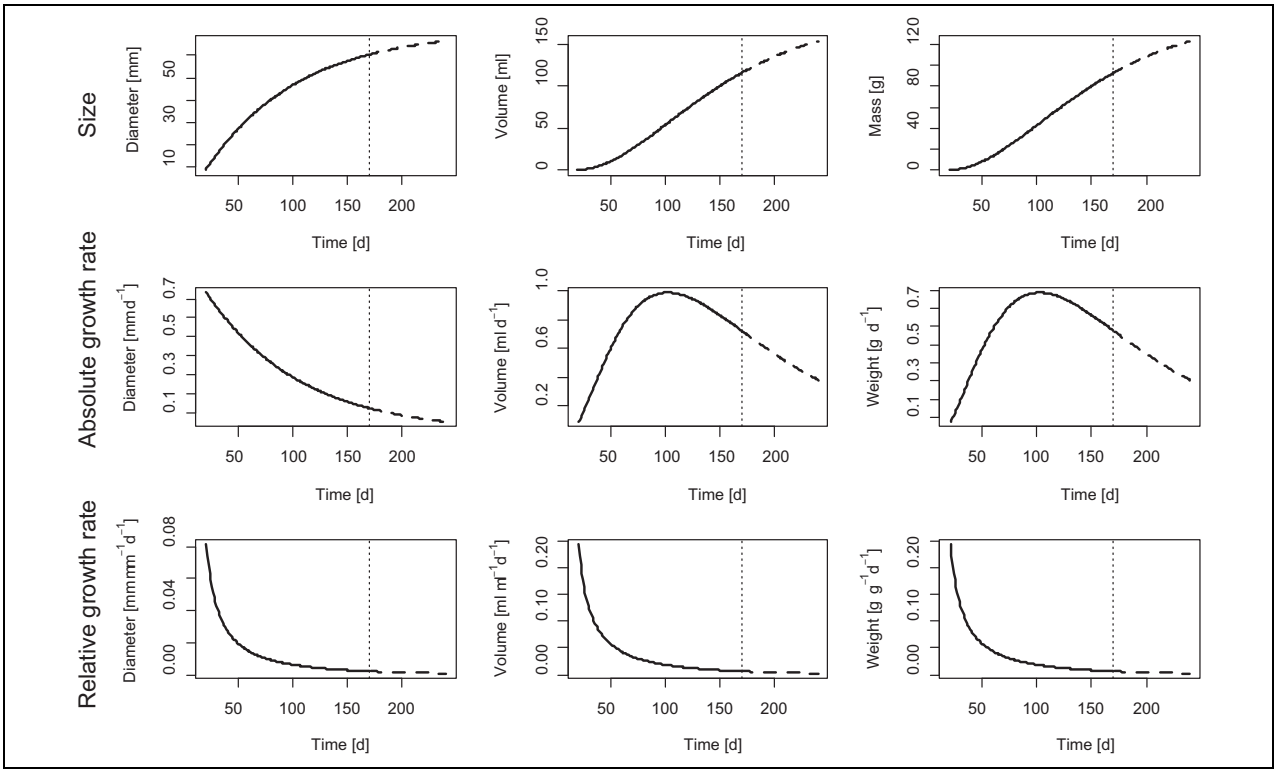


Fig. 4. Curves describing the growth of an average 'Fuji Kiku' apple fruit. Temporal changes of size, absolute and relative growth rate are showed for three measures of growth: diameter, volume and mass. For diameter growth a negative exponential model proposed by VON BERTALANFFY (1938) is used (Equation 1). All other curves result from this curve on the basis of mathematical and physical diameter-volume-mass relationships.

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