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Growth of Individual Tomato Fruits under Assimilate Limitation Associated with Successively-later Set Fruits

M. R. Rybak[1*], K. J. Boote[2] and J. W. Jones[3]

[1]Department of Ecophysiology, EEA INTA (National Institute of Agricultural Technology), Cerro Azul INTA EEA Cerro Azul, Misiones, Argentina.
[2]Department of Agronomy, University of Florida, Gainesville, FL 32611-0500, USA.
[3]Department of Agricultural and Biological Engineering, University of Florida, Gainesville, FL 32611-0500, USA.

Authors' contributions

This work was carried out in collaboration between all authors. Author MRR designed the study, collected the data for the research and wrote the first draft of the manuscript. Authors KJB and JWJ reviewed the experimental design and all drafts of the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

The time course of growth of individual tomato fruits (*Solanum lycopersicum*) was analyzed in relation to the fruit initiation date and cumulative degree days of growth. Experimental data of dry weight (DW), fresh weight (FW), radial diameter (FDIAM), and dry matter concentration (DMC) of three different cohorts of fruits of determinate fresh-market tomato cultivar Florida 47 were determined under field conditions in Florida during spring of 2006 and 2007. Successively later cohorts (1 week intervals) had longer lags prior to rapid growth, slower maximum growth during the rapid phase, and smaller DW, FW, and FDIAM at maturity. These growth patterns were analyzed by fitting the data to a three-parameter Gompertz function for DW, FW, and FDIAM, and to a four-parameter modified Gompertz function for DMC. The good agreement of predicted and measured

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**Corresponding author: E-mail: rybak.maria@inta.gob.ar;*

values indicates that the growth of individual tomato fruits followed the classical S-shaped Gompertz function. The Gompertz function was suitable to describe the slow growth that occurs in tomato fruits immediately after fertilization. The equation was able to predict the increasing duration of this lag and slower maximum growth and smaller final DW, FW, and size for successively later initiated cohorts of fruits. These results confirm the role of sink-source relationships (time of fruit set) on the growth of tomato fruits over time. This study will provide information potentially useful to improve existing tomato crop growth models that are presently limited because they do not predict practical outputs such as fresh weight and size of individual fruits.

Keywords: Tomato; Solanum lycopersicum; fruit dry weight; fruit fresh weight; diameter; fruit dry matter concentration; individual fruit growth equations; gompertz; growing degree days; source-sink effects.

ABBREVIATIONS

Dry Weight (DW); Fresh Weight (FW); Radial Diameter (FDIAM); Dry Matter Concentration (DMC); Thermal time (TT); Mean Square Error (MAE); Standard Error (SE); Days After Tagging (DAT).

1. INTRODUCTION

Theoretical growth functions have been widely used to study plant growth. The construction of growth curves is a valuable tool for dynamic analysis of fruit growth behavior, and growth curves may provide a knowledge base for modeling purposes. Several authors have reported that potential growth of individual tomato fruit under non-limiting conditions exhibits a simple sigmoid or S shaped curve [1-9]. This curve is characterized by three phases. The growth is slow immediately after fertilization, increases gradually to a maximum rate, and finally decreases as the fruit approaches maturation. During the first phase of fruit development, cell division and cell enlargement result in slow growth. Following fertilization, cell division in tomato fruits is activated in the ovary and continues for about 2 weeks [10-12,6,9]. After approximately 2-3 weeks of slow fruit growth, rapid growth begins.

During this time, the fruit cells continue to enlarge by cell expansion. Rapid growth continues for 3 to 5 weeks, culminating in the mature green stage. At this point, the tomato has accumulated the majority of its final weight [28]. Finally, when the biochemical changes related to ripening begin, growth becomes slow again. Approximately 10 days before the first break of color, growth ceases completely. This occurs because an abscission layer is formed between the calyx and the fruit, which becomes a barrier to the transport of water and assimilates to the fruit [9].

The date of fruit initiation strongly affects competition among tomato fruits and the subsequent rates of growth and dry matter allocation to later-set fruits [13]. [14] observed that individual tomato fruit growth is delayed when the competition for assimilates is high, and that delayed fruits started to grow again when the first trusses reached maturity. To explain this phenomenon, [15] used the term “fruit delay” or “fruit latency” to describe fruits that have been set but whose growth and development are delayed during their early stage. These fruits resume their growth after a delay of 10 to 50 days, when the first fruits of the earlier inflorescences have ripened. Moreover, although these delayed fruits come to maturity, their final size is smaller than that of the earlier fruits. Other authors have also observed this fruit growth latency caused by competition for assimilates [16,17,5,14]. [15] experimentally verified that the delay is not produced by parthenocarpy, but is due to competition for assimilates among fruits in a truss and among trusses, with earlier fruits having higher sink strength than later fruits. Tomato fruits initiated at early versus later dates were reported to have significantly different growth rates [18]. While previous research has emphasized equations describing growth of first-formed fruits under non-limiting conditions, we propose that assimilate-limitation is a condition influencing later-set cohorts that has not been adequately described, even if under high N nutrition and full irrigation.

Two equations that are often reported to fit the sigmoid-shaped growth of tomato fruit are the logistic function [18,19,20,21] and the Gompertz function [15,22-25]. The Gompertz function is suitable for a sigmoid growth curve in which growth is frequently not symmetrical about an inflection point, i.e., when the relative growth rate decreases with time [26] as has been shown for tomato by [4]. According to [25], the Gompertz function is more appropriate, because it better accounts for the slow increase in size at the start of the growth period. Examples of mathematical functions used to analyze fruit growth of horticultural crops can be found in [27]. In addition to time, environmental factors having a strong influence on growth may be used to model growth curves.

Any growth variable, e.g. dry weight, fresh weight or fruit diameter, can be plotted as a function of time. Additionally, if growth is analyzed as a function of physiological age of the fruit rather than of calendar time, then temperature is incorporated into the analysis, enhancing the predictive value of the growth functions. The heat unit approach has been used to predict the harvest date of processing tomatoes in California [28,29]. A tool frequently used to estimate the temperature accumulation is growing degree days which are calculated from the daily average temperature minus the base temperature. According to [23], base temperature for fruit development rate and progression to maturity is 5.7ºC while the optimum temperature is 22ºC. Assuming that fruit development rate can be linearly related to temperature, then a critical summation needs to be reached in order for fruits to achieve maturity [9]. [30] proposed that the time from anthesis to maturity for tomato is 806 degree days using a base temperature of 4.75ºC. Using the 4ºC base of [22] this time is 940 degree days.

Temperature is the climatic factor that most affects fruit growth of tomato [31,32]. According to [33] temperature appears to be the principal factor determining the duration of the tomato fruit growth period. His results showed this period to be 73 days at 17ºC and 42 days when temperature increased to 26ºC. Similar results were found by [34]. In his experiment, [33] divided the growth period in five phases, and found different responses to temperature depending on the fruit age. High temperature shortened the growth period in two phases, first at the young developmental state and again close to maturity when temperature had a great impact on days to harvest. The duration of the middle phase of growth was less sensitive to temperature. [23,35] found that when tomato plants were grown at 14, 18, 22 and 26°C, fruits ripened after 95, 65, 46 and 42 days, respectively.

Similarly, [36] found that the time interval from anthesis to harvest was 90 days at 13ºC, 53 days at 19ºC, and 40 days at 26ºC. For these reasons, it is important to evaluate tomato fruit growth as a function of thermal time rather than calendar days.

The relationship between fruit growth rate and temperature has been well studied in tomato [37]. [38] suggested a Q10 value (rate at 10ºC higher temperature compared to initial temperature) equal to 1.7 for tomato fruit growth and equal to 2 for fruit maturation. For fruit growth rate (dry matter and water accumulation) [34] found a temperature optimum of 26ºC while [23] found a regimen of 25/25ºC (day/night) to be optimum for fruit growth rate. [16] found that the maximal rate of dry matter accumulation in tomato fruit at 19.3ºC occurs around day 23 after anthesis (335 degree days using a base temperature of 4.75ºC).

The objective of this study is to examine the time-course of dry matter growth, fresh weight, diameter, and dry matter concentration of individual tomato fruits initiated on different dates during fruit set, and thus exposed to differential C-assimilate stress for plants provided with high N nutrition and optimum irrigation. The ultimate aim of this analysis is generate a knowledge base for simulation purposes to be able to predict individual fruit fresh weight, size, and market quality.

2. MATERIALS AND METHODS

2.1 Field Data

Growth data were obtained from experiments conducted on field-grown, plastic-mulched fresh-market tomato during April to July of 2006 and April to July of 2007 at the University of Florida Plant Science Research and Education Unit at Citra, Florida (29º25’ N, 82º10’ W). The treatment selected for evaluation of fruit growth was well irrigated and fertilized; therefore, no water or nitrogen stress was present at any time during the growing season. The soil at this site is classified as Candler fine sand [39]. This soil contains 97% sand-sized particles and has a field water holding capacity of 0.10-0.12 cm^3 cm^{-3} in the upper 40 cm of the profile [40]. The cultivar evaluated was Florida 47, a mid- to late-season hybrid whose fruits are deep globe shaped.

Field preparation and management is described in detail by [41]. Briefly, the area was rototilled and raised beds (0.30 cm height) were constructed with 1.8 m distance between bed centers. Each replicate plot consisted of four 15.2 m-long rows. Beds were fumigated (80% methyl bromide, 20% chloropicrin by weight) at a rate of 604 kg ha^{-1} after placement of both drip tapes and plastic mulch in a single pass 13 days before transplanting. The 4-wk old plants were transplanted on 4 April 2006 and 7 April 2007. Row spacing was 1.83 m and plant spacing was 0.45 m, making a total of 11,960 plants ha^{-1}. Pre-planting fertilizer application was incorporated into raised beds at a rate of 112 kg of P_2O_5 ha^{-1} and 45 kg of K_2O ha^{-1}. Treatments were replicated four times using a randomized complete block design. Daily irrigation water was applied at a fixed rate of 5.0 to 5.5 mm d^{-1}, in order to meet the evapotranspiration needs of tomato to assure no water stress. Weekly fertigation consisted of injecting dissolved fertilizer salts into fertigation lines according to [42]. All plots received 247 kg ha^{-1} of K as potassium chloride and 12 kg ha^{-1} of Mg as magnesium sulphate. The N-rate corresponded to 330 kg ha^{-1} of N applied as calcium nitrate. The weekly N application rates corresponded to 5.5% of the total N rate applied at wks 1, 2 and 13; 7.1% of the total N rate applied at wks 3, 4 and 12; 8.9% of the total N rate applied at wks 5 to 11.

Irrigation was applied via drip tape (Turbulent Twin Wall, 0.20 m emitter spacing, 0.25 mm thickness, 0.7 L hr^{-1} at 69 kPa, Chapin Watermatics, NY). Climatic data, including temperature, solar radiation, rainfall, wind and humidity were collected by an automatic weather station located within 1 km of the experimental area (Table 1).

2.1.1 Growth analysis of individual fruits

Three sets of flowers separated by one week in age were tagged at anthesis. For each cohort date, at least 60 flowers were tagged in each replicate (modified from [43]). Starting 3 days after anthesis, and two times per week, two tagged fruits in each plot were randomly sampled at 08.00 h. Samples were collected at 3, 7, 11, 15, 19, 23, 27, 31, 35, 39, 43, 47, 51 and 55 days after tagging. For each sampled fruit, the fruit diameter (FDIAM) was measured, the fresh weight (FW) was recorded, and the dry weight (DW) was determined. Treatments were replicated four times using a randomized complete block design. Results were analyzed using the statistical software INFOSTAT. The experimental data on fruit growth (DW, FW, and FDIAM) were fitted to a three-parameter Gompertz function (Eq. 1) in order to analyze the fruit growth as a function of the cumulative degree days (TT) which consider both time and temperature [15,44].

$$Y = \alpha * \exp(-\beta * \exp(-\gamma * TT)) \qquad (1)$$

Where:

Y is the fruit growth in dry weight, fresh weight or fruit diameter
α, β and γ are parameters of the equation TT is cumulative thermal time (degree days)

Cumulative degree days (TT) were calculated from tagging day (0) until first break of color for each cohort (i). Cumulative degree days were calculated by subtracting the base temperature from the daily average temperature (Eq. 2).

$$TT = \sum_{0}^{i} \left[\frac{(T_{\max} - T_{\min})}{2} \right] - T_b \qquad (2)$$

Where

T_{max} is the maximum daily temperature
T_{min} is the minimum daily temperature
T_b is the base temperature for fruit growth equal to 5.7°C

The data on fruit dry matter concentration (DMC) were fitted to a four-parameter Gompertz function with displacement, for pattern of DMC variation versus cumulative degree days (Eq. 3).

$$DMC = \alpha * \exp(-\beta * \exp(-\gamma * TT)) + \delta \qquad (3)$$

Where:

DMC is the fruit dry matter concentration in percentageα, β,γ, and δ are parameters of the equation.

Table 1. Weather data recorded within 1 km of the experimental area in Gainesville FL during spring of 2006 and spring of 2007 (each value is an average of 10 days data)

Period	Tavg (2m)	Tmin (2m)	Tmax (2m)	Solar radiation	Total rain (10 days)
	°C	°C	°C	MJ d-1	mm
2006					
04/01-04/10	20.7	13.5	28.3	20.4	41.4
04/11-04/20	21.9	16.0	28.9	20.6	0.5
04/21-04/30	22.9	17.3	29.3	19.8	9.9
05/01-05/10	23,3	16.6	31.0	22.1	4.8
05/11-05/20	22.3	15.1	29.4	20.9	3.6
05/21-05/31	26.3	19.8	34.2	20.1	3.3
06/01-06/10	25.2	19.1	32.2	18.9	1.8
06/11-06/20	25.8	21.4	31.3	16.3	9.8
06/21-06/30	30.9	25.8	37.7	20.4	1.3
07/01-0710	26.2	20.7	32.4	19.3	9.2
2007					
04/01-04/10	17.7	11.5	22.6	16.9	7.9
04/11-04/20	19.6	12.1	27.6	21.2	59.4
04/21-04/30	21.6	14.0	29.0	27.9	0.0
05/01-05/10	22.9	16.2	30.2	19.6	0.0
05/11-05/20	22.8	16.1	30.1	21.2	2.0
05/21-05/31	27.5	19.8	35.2	21.3	2.0
06/01-06/10	25.5	20.8	31.6	19.7	51.3
06/11-06/20	25.4	20.1	31.9	18.9	35.1
06/21-06/30	26.5	21.7	32.8	20.5	24.4
07/01-0710	27.1	23.1	33.1	25.0	61.7

3. RESULTS AND DISCUSSION

3.1 Measured Fruit Growth

The observed final fresh weight, dry weight and fruit diameter of fruits whose development began on different tagging dates during the years 2006 and 2007 are presented in Table 2. Means and standard deviations are shown in appendix 1 (2006) and 2 (2007).The total dry and fresh weight differed significantly among cohorts. Fruits that developed from flowers tagged earlier (first cohort) achieved the highest mass (both dry and fresh). Fruits from the second cohort achieved lower final mass than the first cohort, but higher final mass than the third cohort. The differences between cohorts 1 and 2, and 2 and 3, are the result of progressively delayed and slower growth of the later-set fruits. The DW of cohort 3 was 26 to 58% of the DW of cohort 1, depending on year.

These differences among cohorts in the final fresh and dry weights are partly attributable to differences in the length of the fruit growth period, which was 55 calendar days for cohort 1, 47 calendar days for cohort 2 and 39 calendar days for cohort 3, nearly same in both years (data not shown). The cumulative thermal time was 991 and 1033 degree days for cohort 1, 857 and 898 degree days for cohort number 2, and 720 and 747 degree days for cohort number 3 from tagging to first break color during 2006 and 2007, respectively. Others authors have been used time from fruit set in growth functions as a reasonable predictor of fruit growth over time. [23] (size); [45] (fresh and dry weight).Although physiological processes underlying the differences among cohorts growth pattern need further research our results agreed with [16]. He established that the partitioning of dry matter in tomato is regulated by competition for leaf assimilates and showed how these competition among fruits is regulated by different stages of inflorescences development (earlier vs. later fruits).

Fruits of the first cohort reached higher final mass accumulation (DW and FW) during 2007 than in 2006 (Table 2). This could be the result of cooler temperature and higher solar radiation during growth of the first cohort in 2007 than 2006 (Table 1). On the other hand, the third cohort reached small final mass in 2007 than in 2006.

Table 2. Comparison among three cohorts for dry weight (DW), fresh weight (FW), dry matter concentration (DMC) and fruit diameter of individual tomato fruits measured at maturity during the spring of 2006 and 2007 at Gainesville, FL. each value is the mean of eight fruits (two per replication)

Cohort	2006	2007
Dry weight	- - - - - - - - - - -g fruit $^{-1}$- - - - - - - - - - -	
1st cohort	10.8 a	13.6 a
2nd cohort	7.9 b	9.1 b
3rd cohort	6.3 c	3.6 c
Fruit weight	- - - - - - - - - - -g fruit $^{-1}$- - - - - - - - - - -	
1st cohort	224 a	279 a
2nd cohort	173 b	172 b
3rd cohort	154 c	72 c
Dry matter conc.	- - - - - - - - - - - - % - - - - - - - - - - - -	
1st cohort	4.8 a	5.0 a
2nd cohort	4.7 a	4.9 a
3rd cohort	4.9 a	4.8 a
Fruit diameter	- - - - - - - - - - - - cm - - - - - - - - - - - -	
1st cohort	9.0 a	10.4 a
2nd cohort	7.2 b	7.5 b
3rd cohort	3.9 c	3.3 c

† Means within columns followed by the same lowercase letters are not significantly different ($P \leq 0.05$) according to duncan's multiple range test for cohorts within same season

3.1.2 Gompertz equations and time course of fruit dry weight and fresh weight

The time-courses of observed DW, FW, FDIAM, and DMC for individual tomato fruits are plotted along with their fitted Gompertz equations in Fig. 1 for 2006, and in Fig. 2 for 2007. The two years show relatively repeatable responses, particularly showing the different growth patterns between the successively later-formed cohorts 1, 2, and 3 in each year. The solved parameters for the Gompertz functions are given in Table 3 for 2006 and Table 4 for 2007. The growth of tomato fruits in DW, FW and diameter was well described by the Gompertz function. The best relationship was for cohort 1. Cohorts 1, 2 and 3 have a similar mean square error (MAE) and standard error (SE) for the coefficients α and γ; however, the SE of the parameter β was higher for cohorts 2 and 3 (Tables 3 and 4), showing that β is the parameter with the greatest uncertainty. The parameter α closely followed the final fruit dry weight, fresh weight or diameter which was progressively decreased for later-set fruits. The parameter α showed differences among cohorts in both years, but the range was greater, nearly twofold difference in 2007 (Tables 3 and 4). Tomato fruits showed the classical sigmoid growth curve, albeit with a nearly linear middle phase. Growth began with a phase of slow growth for a few days after anthesis, then increased to an almost linear slope for about 4 to 5 weeks, and then slowed again close to maturation. The curves are largely convex, but have a lag period lasting between 80 and 260 growing degree days, with the lag period increasing for later cohorts. Similar results were obtained when the 2007 data was fitted to a Gompertz function (Table 4 and Figs. 2A, B, C).

There were differences among cohorts in the rate of growth. The rate of dry mass accumulation estimated from the first derivative of the Gompertz function showed that the three cohorts did not have the same growth rate. Similar trends were observed in both years, but 2007 results will be discussed. For instance, in 2007, the maximum growth rate was reached relatively earlier in cohort 1, occurring on day 22, which represents about 40% of the total growth period. Cohort 2 also reached the maximum growth rate on day 22, representing about 45% of the total fruit growth period. [15,46] similarly reported that the maximum growth rate in tomato fruits was reached by day 21 to 25 after anthesis. A larger lag was observed in cohort 3. For this cohort, the maximum growth rate occurred on day 26, after almost 63% of the total fruit growth period. Figs. 1A, 1B, 1C (2006) and Figs. 2A, 2B, and 2C (2007) shows how the later set fruits, had longer initial lag phase, but still reached a relatively high maximum growth rate during their phase of rapid growth. Reported values of tomato fruit maximum growth rate range from 0.20 g dry matter d^{-1} [47]

to 0.37 g dry matter d^{-1} [46,48] reported a value as high as 1.04 g dry matter d^{-1}. Variation in growth rate among cohorts has also been reported by [18,5,15],who found that the rate of dry matter accumulation was significantly different among fruits initiated on different dates. In our study averaging 2006 and 2007 data, maximum fruit growth rate was 0.40, 0.36 and 0.29 g dry matter d^{-1} for cohorts 1, 2, and 3 respectively.

3.1.3 Fruit dry matter concentration over time and gompertz function

The final fruit dry matter concentration was similar for the three cohorts (Table 2). However, the DMC data of both years were fit better with a four-parameter Gompertz function with displacement (Figs. 1D and 2D) than with a simple Gompertz function. The modified Gompertz function was needed because the pattern of dry matter concentration varied among cohorts, and this variation was related to the timing of fruit initiation, with a longer lag prior to growth being associated with a longer period of sustained relatively higher DMC (Figs. 1D and 2D). The DMC rapidly decreased until about 550 growing degree days were accumulated and then plateaued consistent with the trend in FW and DW. These results are consistent with the published by [49]. They used an equation of DMC vs. TT and indicated the decline in DMC over time as well as final values of DMC at fruit maturity from 12.5 to 5%. The Gompertz parameters for the DMC function are given in Tables 3 and 4.

3.1.4 Fruit size

The mean final fruit size differed significantly among cohorts, as shown in Table 2 and Figs. 1C and 2C for years 2006 and 2007. Fruits that developed from flowers tagged earlier achieved the greatest diameter. The fruits that developed from the second cohort achieved smaller diameters than the first cohort, but were larger than fruits from the third cohort. These differences are attributable to the same factors proposed to explain the differences among cohorts in final fresh and dry weights. Fruits from cohort 3 in the 2007 season did not reach commercial size while fruits in cohort 3 in 2006 reached commercial size although it corresponded to an extra small class size, according to the U.S standard class size for fresh market tomatoes [50].

Table 3. Estimated coefficients solved by fitting the 2006 data to a gompertz function to predict DW, FW and fruit diameter vs. thermal time and to a gompertz function with displacement to predict fruit DMC vs. thermal time

Parameter	**Fruit dry weight (g) = alpha*exp(-beta*exp(-gamma*TT))**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	10.79	0.32	7.68	0.08	7.05	0.16
β	6.85	1.34	56.0	14.0	3675	2861
γ	0.01	5.9E-04	0.01	7.7E-04	0.02	3.1E-04
Parameter	**Fruit fresh weight (g) = alpha*exp(-beta*exp(-gamma*TT))**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	241	10.54	178	1.71	139	5.83
β	15.50	1.21	45	5.56	316	364
γ	0.01	4.5E-03	0.01	5.0E-04	0.02	3.2E-03
Parameter	**Fruit diameter (cm) = alpha*exp(-beta*exp(-gamma*TT))**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	9.91	0.50	7.15	0.10	4.97	0.10
β	5.98	1.02	20.3	4.73	2430	2122
γ	0.004	4.1.0E-04	0.01	8.1E-04	0.02	2.4E-03
Parameter	**Fruit DMC (%) = alpha*exp(-beta*exp(-gamma*TT))+δ**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	12.21	2.86	12.29	0.68	7.21	0.90
β	1.74	0.75	0.28	0.04	0.05	0.03
γ	-0.0014	4.9E-04	-0.01	3.5E-04	-0.01	3.4E-03
δ	4.75	0.15	4.68	0.05	5.25	0.20

Table 4. Estimated coefficients solved by fitting the 2007 data to a gompertz function to predict DW, FW and fruit diameter vs. thermal time and to a gompertz function with displacement to predict fruit DMC vs. thermal time

Parameter	Fruit dry weight (g) = alpha*exp(-beta*exp(-gamma*TT))					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	15.0	0.59	9.17	0.08	4.29	0.41
β	4.7	0.64	54.7	46.8	39.18	22.66
γ	0.0045	4.6E-04	0.01	2.5E-03	0.01	1.0E-03
Parameter	**Fruit fresh weight (g) = alpha*exp(-beta*exp(-gamma*TT))**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	309	9.71	182	5.53	87.8	5.87
β	15.50	0.9	93	66.7	81.0	50.67
γ	0.005	4.1E-04	0.01	2.0E-03	0.01	1.5E-03
Parameter	**Fruit diameter (cm) = alpha*exp(-beta*exp(-gamma*TT))**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	11.32	0.36	7.69	0.21	4.63	0.10
β	6.43	0.89	23.0	8.0	18.62	10.1
γ	0.01	4.8.0E-03	0.01	1.1E-03	0.01	1.6E-03
Parameter	**Fruit DMC (%) = alpha*exp(-beta*exp(-gamma*TT))+δ**					
	Cohort 1	**S.E**	**Cohort 2**	**S.E**	**Cohort 3**	**S.E**
α	16.2	5.0	13.94	8.9	8.13	0.98
β	0.89	0.5	0.41	0.05	0.09	0.07
γ	-0.005	7.7E-04	-0.0042	3.0E-0.4	-0.01	2.0E-03
δ	4.57	0.19	4.34	0.05	5.25	0.23

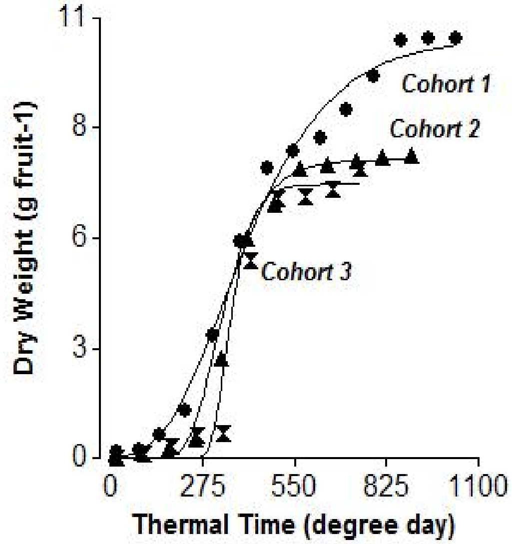

Fig. 1A. Individual fruit growth curves (g dry matter per fruit) over time in 2006, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

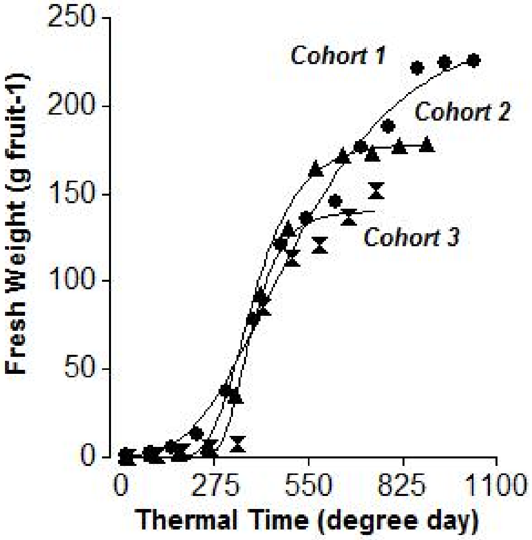

Fig. 1B. Individual fruit growth curves (fresh weight per fruit) over time in 2006, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

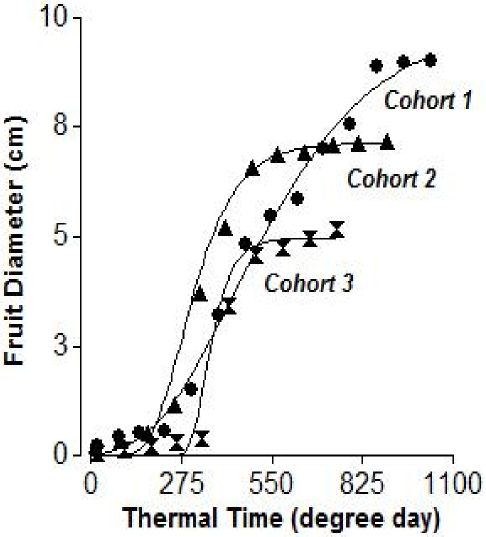

Fig. 1C. Individual fruit growth curves (fruit diameter) over time in 2006, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

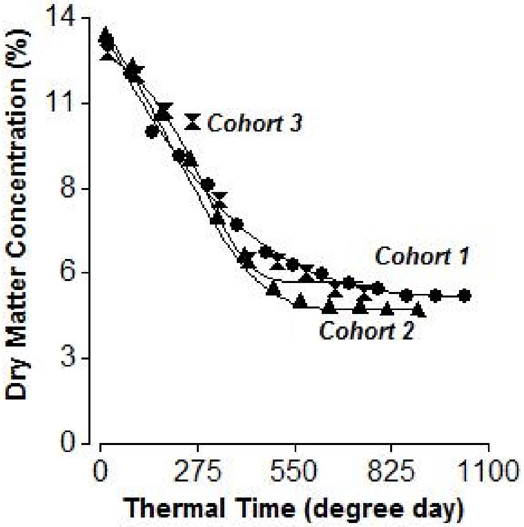

Fig. 1D. Individual fruit dry matter concentration over time in 2006, fitted to a four-parameter inverse gompertz function. Each point is a mean of four fruits

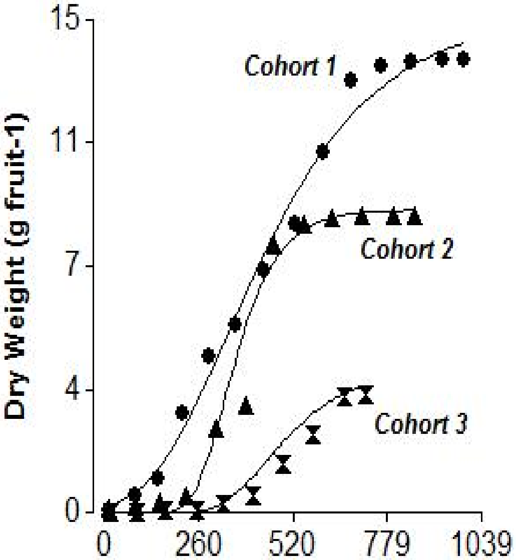

Fig. 2A. Individual fruit growth curves (g dry matter per fruit) over time in 2007, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

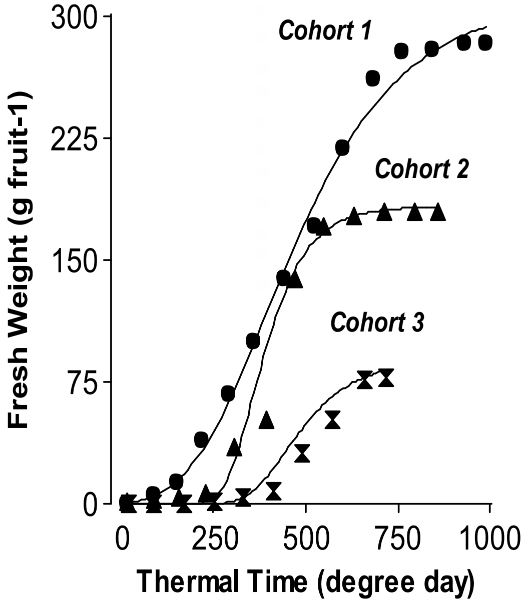

Fig. 2B. Individual fruit growth curves (fresh weight per fruit) over time in 2007, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

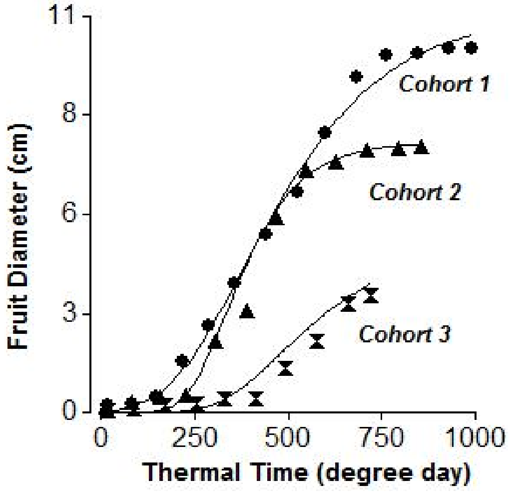

Fig. 2C. Individual fruit growth curves (fruit diameter) over time in 2007, fitted to a three-parameter gompertz function. Each point is a mean of four fruits

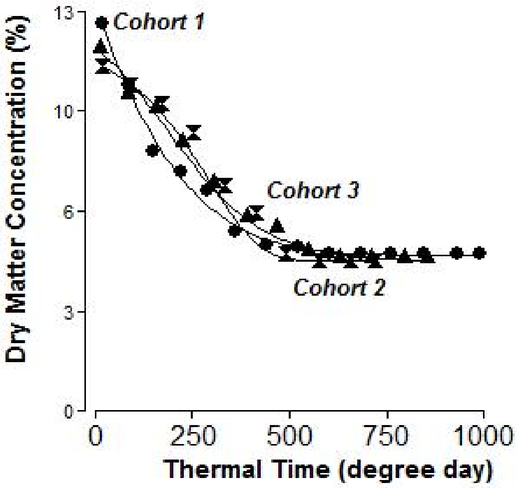

Fig. 2D. Individual fruit dry matter concentration over time in 2007, fitted to a four-parameter inverse gompertz function. Each point is a mean of four fruits

4. CONCLUSION

The growth of individual tomato fruits expressed in terms of dry weight, fresh mass or fruit size followed a sigmoid curve, and was well represented by a three-parameter Gompertz function. This function was adequate to reproduce the lag in the growth of tomato fruits early in the cycle (between one and two weeks after anthesis, depending on the cohort). Differences in growth patterns were mainly related to the timing of initiation of the fruits, which determined the duration of the growth period, the lag period prior to rapid growth, and the maximum rate of rapid growth. The sink strength of earlier-set fruits was clearly stronger than that of later-set fruits.

The influence of carbon assimilate shortage associated with later-set fruit cohorts (with high N nutrition and optimum irrigation) contributed to a longer lag phase, a slower growth rate, and a shorter total fruit growth duration. The transition from lag phase to rapid growth for cohort 3, in at least one of the years, seemed to be associated with the slowing of growth of cohort 1, as if sink requirement for assimilate had been relieved. The Gompertz equations, while individually predictive of growth of each cohort, had different coefficients per cohort which would make it difficult to use one set of Gompertz coefficients to predict the variation in fruit growth (lag, rate, and total growth duration) and market size associated with progressively later-set fruits. This shortcoming may be partially solved by use of dynamic crop growth models that consider assimilate supply and current sink strength of fruits relative to progressively later-set fruits, and use those aspects to regulate individual fruit growth characteristics (lag, rate, and duration).These results of growth patterns and particular equations are valid for the Florida 47 cultivar studied in our experiment, and we recognize that fruit growth patterns could differ for other genotypes including exotic and mutant germplasm

The dry matter concentration was better represented by a four-parameter Gompertz function with displacement than by the classical three-parameter Gompertz function. This allowed a better description of the lag period during which the DMC remained high prior to the onset of rapid fruit growth. This aspect would work even better, if linked with a dynamic crop model that predicts the lag period, and thus holds the DMC high until rapid growth begins.

Data from this study is anticipated to be useful as base knowledge to improve existing dry matter-based tomato growth models where FW, DMC and fruit size are not predicted despite the practical applications of such predictions. This is important because the growth of individual fruits in FW and size determines both fruit quality and total yield of fresh market tomatoes.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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APPENDIX

Appendix 1. Mean and standard deviation (S.D) of growth variables of tomato fruits measured every 3 days after tagging (DAT) during spring of 2006 in Gainesville Florida (each value is a mean of four fruits)

DAT	Cohort	DW (g fruit^{-1})	S.D	FW (g fruit^{-1})	S.D	DMC %	S.D	DIAM cm	S.D
3	1	0.10	0.012	0.8	0.12	13	1.21	0.23	0.02
7	1	0.67	0.087	5.6	0.12	12	0.27	0.44	0.01
11	1	1.32	0.07	13	0.12	10	0.49	0.52	0.02
15	1	2.1	0.14	23	0.87	9.3	0.42	0.66	0.01
19	1	3.12	0.26	37	3.97	8.4	0.17	1.5	0.10
23	1	5.6	0.61	78	5.62	7.1	0.38	3.2	0.16
27	1	7.5	0.35	120	5.2	6.2	0.09	4.84	0.25
31	1	7.9	0.28	136	7.56	5.8	0.2	5.5	0.33
35	1	8.3	0.72	146	8.1	5.5	0.13	5.9	0.6
39	1	8.9	0.75	176	10.1	5.2	0.13	7	0.54
43	1	9.7	0.84	189	11	5	0.11	7.6	0.9
47	1	10.4	0.67	221	11.2	4.8	0.13	8.8	0.87
51	1	10.7	0.85	223	14	4.8	0.5	8.9	0.12
55	1	10.8	0.94	224	12	4.8	0.3	9	0.14
3	2	0.04	0.0005	0.37	0.06	13.2	1.31	0.15	0.03
7	2	0.09	0.012	0.7	0.12	12.1	0.26	0.28	0.05
11	2	0.13	0.014	1.2	0.20	10.7	0.47	0.47	0.08
15	2	0.5	0.06	4.9	0.86	9.2	0.41	1.1	0.19
19	2	2.51	0.17	34	4.16	7.3	0.19	1.4	0.52
23	2	5.6	0.39	92	9.66	6.1	0.36	3.7	0.73
27	2	6.4	0.46	129	13.61	5	0.33	5.2	0.75
31	2	7.4	0.59	163	17.19	4.9	0.25	6.5	0.69
35	2	7.6	0.54	167	13.68	4.8	0.22	6.8	0.69
39	2	7.2	0.4	170	13.8	4.7	0.22	6.9	0.54
43	2	7.7	0.36	172	9.8	4.7	0.22	7	0.5
47	2	7.9	0.38	173	8.7	4.7	0.22	7.2	0.5
3	3	0.09	0.01	0.08	0.004	12.7	1.11	0.05	0.003
7	3	0.1	0.015	0.92	0.05	11.9	0.36	0.12	0.01
11	3	0.3	0.06	2.76	0.15	10.8	0.54	0.22	0.01
15	3	0.57	0.08	5.5	0.3	9.3	0.45	0.32	0.02
19	3	0.61	0.075	14	0.42	7.9	0.37	0.37	0.02
23	3	2.1	0.11	85	4.63	6	0.22	3.42	0.19
27	3	3.8	0.21	113	6.17	5.8	0.22	3.5	0.25
31	3	4.5	0.29	121	6.41	5.6	0.21	3.7	0.26
35	3	6.1	0.33	137	7.26	4.9	0.23	3.9	0.28
39	3	6.3	0.41	154	8.4	4.9	0.25	3.9	0.28

Appendix 2. Mean and standard deviation (S.D) of growth variables of tomato fruits measured every 3 days after tagging (DAT) during spring of 2007 in Gainesville Florida (each value is a mean of four fruits)

DAT	Cohort	DW (g fruit^{-1})	S.D	FW (g fruit^{-1})	S.D	DMC %	S.D	DIAM cm	S.D
3	1	0.07	0.01	0.59	0.05	12.4	0.91	0.06	0.078
7	1	0.54	0.05	3.2	0.47	10.4	0.87	0.15	0.021
11	1	1.03	0.09	12.4	1.12	8.3	0.61	0.25	0.045
15	1	2.98	0.27	67.3	6.06	7.6	0.53	1.35	0.216
19	1	4.71	0.42	99.8	8.99	7	0.61	2.6	0.32
23	1	5.69	0.51	139	12.6	5.7	0.45	4.3	0.56
27	1	7.35	0.66	171	16	5.3	0.43	5.86	0.68
31	1	8.73	0.79	218	22.3	5.1	0.6	7.2	0.65
35	1	10.9	0.98	261	27	5	0.63	8.89	0.72
39	1	13.0	1.02	270	25.3	5.0	0.23	9.97	0.87
43	1	13.1	0.95	273	28.0	5.0	0.22	10.2	0.71
47	1	13.3	0.96	275	23.7	5.0	0.22	10.3	0.74
51	1	13.5	0.96	278	27.3	5.0	0.25	10.35	0.73
55	1	13.6	0.96	279	29.0	5.0	0.24	10.4	0.68
3	2	0.04	0.004	0.31	0.04	11.6	1.16	0.13	0.02
7	2	0.10	0.01	0.98	0.12	10.1	1.30	0.12	0.03
11	2	0.28	0.03	2.9	0.37	9.7	1.21	0.22	0.05
15	2	0.46	0.05	5.3	0.66	8.6	0.93	0.37	0.07
19	2	2.52	0.29	34	4.27	7.3	0.82	1.38	0.25
23	2	3.17	0.21	51	6.37	6.2	0.77	2.10	0.30
27	2	6.25	0.52	136	12.7	5.9	0.56	5.50	0.46
31	2	8.08	0.56	160	14.62	5.1	0.66	6.82	0.56
35	2	8.65	0.58	163	14.12	5	0.52	7.00	0.59
39	2	8.80	0.61	168	15.1	4.9	0.50	7.4	0.67
43	2	8.95	0.66	170	13.29	4.9	0.57	7.48	0.55
47	2	9.1	0.70	172	14.86	4.9	0.61	7.5	0.61
3	3	0.033	0.0003	0.03	0.0005	11.6	1.7	0.05	0.008
7	3	0.048	0.0003	0.19	0.0032	10.4	1.6	0.11	0.021
11	3	0.08	0.0012	0.49	0.012	9.9	1.1	0.17	0.036
15	3	0.198	0.0038	0.9	0.016	8.9	0.92	0.20	0.033
19	3	0.251	0.01	3.49	0.31	7.2	0.67	0.37	0.10
23	3	0.521	0.02	8.28	7.4	6.3	0.69	0.41	0.16
27	3	1.452	0.15	32	3.3	5.6	0.43	1.27	0.03
31	3	2.39	0.05	52	4.2	4.8	0.80	2.00	0.33
35	3	3.51	0.03	66	5.70	4.8	0.67	3.10	0.55
39	3	3.6	0.02	72	3.17	4.8	0.89	3.3	0.70

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