# A Functional and Exploratory Approach to Studying Growth: The Example of the Peach Fruit

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*Abstract.* An approach to studying fruit growth is presented for peach fruit (*Prunus persica* L. Batsch). It combines a functional description of growth curves, multivariate exploratory data analysis, and graphical displays. This approach is useful for comparing growth curves fitted to a parametric model, and analysis is made easier by the choice of the model whose parameters have a meaning for the biologist. Growth curves were compared using principal component analysis (PCA) adapted to the table of estimated parameters. Growth curves of 120 fruits were fitted to a model that assumes two growth phases. The first one described the pit growth and the first part of the flesh growth. The second described the second part of the flesh growth. From PCA, firstly it was seen that fruit growth varied according to cumulated growth during both growth phases and to date of maximal absolute growth. Secondly, fruit growth varied according to cumulated growth and relative growth rates during each phase. Further examples are presented where growth curves were compared for varying fruit number per shoot and leaf : fruit ratio, and for different sources of variation (tree, shoot, and fruit). Growth of individual fruit was not related to fruit number per shoot or to leaf : fruit ratio. Growth variability was especially high between fruit within shoots.

Progress in fruit production depends on our ability to study fruit growth, which is difficult because the fruit population within a tree is very large. Moreover, growth is not a linear function of time, and there is a high variability in the population of fruits. Thus, methodological approaches are needed to manipulate many growth curves and the various components of fruit growth and patterns in the data sets to be identified. Growth curves have been extensively described and analyzed for many years (Causton and Venus, 1981). Classical techniques involved calculating absolute or relative growth rates from raw data over various periods of time (Radford, 1967). The functional approach is another possibility. Here, a function is fitted to growth data and, if the values of its parameters can be interpreted from a biological point of view, the growth curves can be compared more easily than in the classical approach. The technical advantages of this approach have been pointed out by Hunt (1981). For example, small deviations from the original experimental data's general trend are smoothed out, making the final results less erratic. Moreover, the continuity of the model allows derived quantities (absolute and relative growth rate for example) on each point of the model curve to be obtained. Multivariate exploratory analysis, although rarely used in horticultural research (Iezzoni and Pritts, 1991), is of interest in studying growth curves typified by several parameters. Methods such as these are useful for exploring multivariate data and putting forward hypotheses on their structure. Several authors (Carrel et al., 1986; Weihs and Schmidli, 1990) have enhanced the multivariate exploratory approach by applying graphical methods; thus, these are powerful tools for seeking structures in data sets. We present an approach corresponding to the abovementioned aims, that combines a functional description of growth curves, multivariate exploratory data analysis, and graphical methods. We used this approach in comparing cumulated growth and absolute growth rate between peaches within an orchard. The results were used to study the effect of fruit count per shoot, the leaf : fruit ratio on peach growth, and to evaluate the variability of fruit growth between and within trees.

### Materials and Methods

### Sample data set

The fruits were grown on twelve g-year-old peach trees (Prunus persica L. Batsch) planted in an orchard at the the Institut National de la Recherche Agronomique (INRA), Avignon. The cultivar used was the late-maturing 'Suncrest'. Trees were goblet-trained and received routine horticultural care. The mean yield of studied trees was 21 kg/tree, which was a low crop load since it could reach 45 kg/tree per year. A south exposed branch was chosen on each tree. Only four 1-year-old shoots of 25 to 120 cm (mean 80 cm) were kept on the branch that constituted the unit on which a single treatment was applied. We kept 20 fruits for each unit. The four treatments were defined controlling their fruit count : shoot and lateral shoot count : fruit ratios (Table 1). The leaf : fruit ratio increased from May to July (Table 1). Weekly measurements of cheek diameter were made between 28 Apr. (44 days after full bloom) and 26 July 1989 (beginning of harvest) on 192 fruits of the 240 kept on the shoots. Within them, 120 were harvested and studied because of a drop of  $\approx 38\%$  fruit in all treatments.

#### The functional and exploratory approach

*Modeling growth curves.* The typical growth curve of peach fruit is a double sigmoid and may be divided into three periods: one of rapid growth, another of much slower growth, and a last period of rapid growth (Connors, 1919). Pit and flesh growth contribute to the first period and flesh growth alone to the third

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Abbreviation: PCA, principal component analysis.

Table 1. Distribution of fruits on the four shoots of each treatment, lateral shoots count per fruit and leaf count per fruit.

Treatment	Repetition	ion Fruit count		t	Lateral shoot count	Leaf con	count : fruit	
Treatment	01 tiees		. 5110	501		. IIuIt	May 9	July 21
1	3	10	10	0	0	2	14	165
2	3	5	5	5	5	2	14	116
3	3	10	10	0	0	1	7	81
4	3	5	5	5	5	1	7	63

(Zucconi, 1986). During the second period, the pit reaches its maximum diameter and flesh growth is slow. Like Baker and Davis (1951) and Dejong and Goudriaan (1989), we assumed the cumulated growth of peaches to be according to a two phase growth characterized by a two growth-curve model. The first model, which especially describes pit and flesh growth during the first period, is represented by a monomolecular function, and the second, which particularly describes flesh growth during the third period, by a logistic function. The second period corresponds to the overlapping of the two growth curves. Diameter increase Y was modeled between 28 Apr. ( $t_o = 0$  day) and 26 July 1989  $(t_1 = 89 \text{ days})$ . The model is  $Y(t,\Theta) = p_1(1 - p_2t) + p_3/(1 + e^{-p_4(t-p_5)})$  where t is time, varying between  $t_0$  and  $t_1$  days, and  $\Theta = (p_1, p_2, p_3, p_4, p_5)$  a set of parameters. The above model has two advantages: 1) the summation of two expressions can be associated with our knowledge of the phases of fruit growth, and 2) interesting events of the model curve are simple expressions of parameters and have a biological meaning. Among the parameters,  $p_1$  was cumulated growth, especially during the first phase. Fruits with high  $p_1$  had good growth

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conditions during this phase;  $p_2$  was the relative growth rate  $\frac{dY}{dt}(t_0,\Theta)/p_1$  at the beginning of the study. Fruits with high  $p_2$  rapidly reached the maximal cumulated growth  $p_1$ . Parameter  $p_3$  was similar to  $p_1$  for the second period;  $p_4$  was proportional to the relative growth rate $(p_5,\Theta)/p_3$  at  $p_5$ , which was the date

of maximal absolute growth rate during the second period. Fruits with high  $p_4$  rapidly reached the maximal cumulated growth  $p_3$  during the second period (Fig. 1A-C). The absolute growth rate curves  $\frac{dY}{dt}(t,\Theta)$  were found by deriving  $Y(t,\Theta)$  with respect to t

(Fig. 1D). For each fruit, the parameters were fitted by the least squares method (Bard, 1974).

Method used for the comparison of the growth curves. Houllier (1987), using a parametric growth model  $Y(t,\Theta)$ , depending on time t and parameters:  $\Theta$ , proposed a distance between growth curves as equal to the mean square deviation between them. Let  $\Theta^{(i)} = (\Theta_i^{(i)}, \dots, \Theta_k^{(i)})^T$ ,  $i = 1, \dots, n$ , be the estimated parameters of n curves. The Euclidean distance between two curves i and j over time interval  $[t_0, t_1]$  is defined by

$$dist^{2}(i,j) = \int_{t_{0}}^{t_{1}} (Y(t,\Theta^{(i)}) - Y(t,\Theta^{(j)}))^{2} dt \qquad [1]$$

Examples of the value of distance between curves are given in Fig. 2 for cumulated growth and in Fig. 3 for absolute growth rate.

Expanding  $Y(t, \Theta^{(i)})$  about  $\Theta = \overline{\Theta}$ , where  $\overline{\Theta}$  is the vector of the sample mean parameters  $(\overline{\theta_1}, ..., \overline{\theta_k})^T$ , we obtain a linear approximation *YY* of *Y* at time *t* 

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Fig. 1. Modeling of cumulated growth (A-C), and absolute growth rate (D).



Fig. 2. Distances between cumulated growth of fruits given in Table 2.

$$Y(t,\Theta^{(i)}) \simeq \tilde{Y}(t,\Theta^{(i)}) = Y(t,\overline{\Theta}) + \sum_{1=1}^{k} \frac{\partial Y}{\partial \theta_{1}}(t,\overline{\Theta}) \cdot (\theta_{1}^{(i)} - \overline{\theta}_{1}) \quad [2]$$

 $\partial Y/\partial \theta_1$  being the derivative of Y with respect to  $\theta_1$ .

Substituting for this development into Eq. [1] yields

$$dist^{2}(i,j) \approx (\Theta^{(i)} - \Theta^{(j)})^{\mathrm{T}} M(\Theta^{(i)} - \Theta^{(j)}), \qquad [3]$$

where *M* is a  $k \times k$  symmetric matrix defined by

$$M_{\rm rs} = \int_{t_0}^{t_1} \frac{\partial Y}{\partial \theta_{\rm r}}(t,\overline{\Theta}) \frac{\partial Y}{\partial \theta_{\rm s}}(t,\overline{\Theta}) dt \quad r = 1, k \text{ and } s = 1, k.$$
 [4]

If *Y* is sufficiently regular, *M* is definite positive. Equation [3] means that the distance between two curves is roughly equal to the distance defined by *M* by means of their respective parameters. The elements  $M_{rs}$  can be computed using numerical methods.

The matrix M used to calculate the distance between cumulated growth curves  $Y(t,\Theta)$  differs from that used for absolute growth rate curves  $dY(t,\Theta/dt$ . It was calculated by replacing Y with dY/dt in Eqs. [1], [2], and [4]. Three conditions are required to make good use of the method. First, to ensure proper interpretation of parameters, goodness-of-fit to the data of each estimated growth curve was tested by percentage of explained variance. Second, computation of the distance between cumulative growth curves (absolute growth curves, respectively) required the goodness of approximation of  $Y(t,\Theta)$  ( $dY(t,\Theta)/dt$ , respectively) by the linear function of the parameters  $\bar{Y}$  at any time *t*. We estimated this goodness of approximation by the ratio *E* of the mean quadratic error by the mean growth, i.e.,

$$E = \frac{1}{(t_1 - t_0)m} \int_{t_0}^{t_1} (Y(t, \Theta) - \tilde{Y}(t, \Theta))^2 dt$$

where *m* is the mean daily cumulated growth during  $(t_0, t_1)$ . We computed E for the absolute growth rate curves in the same way. The third condition concerns the interpretation of the curve's variability (cumulative or absolute growth) within the population of fruit by means of the parameters. The estimations of parameters of a fruit have a variance resulting from fitting raw data to the model. The parameters of all fruits have also a variability within the population of fruits. So, we verified that the ratio of the variance of the estimations of parameters on each fruit by the variance of the parameters within the population of fruits was low. PCA was used to compare fruit growth by means of the estimated parameters. Information about PCA is presented for horticultural researchers by Iezzoni and Pritts (1991), but we summarize the main ideas of the method to enhance understanding of the adaptation we propose. The goal of PCA is to summarize a multivariate data set as accurately as possible using a few uncorrelated components ranked by that part of the variance of data they explain. The multivariate data analyzed are presented in a table that has as many rows as fruits and whose five columns contain the estimations of the five parameters (Table 2). PCA needs a matrix to compute the Euclidean distance between the rows of the table. Usually it is the identity matrix, but any symmetric definite positive matrix can be used to create a distance (Lebart et al., 1984). We used the specific M matrices, defining distances between curves, for cumulative growth and absolute growth rates. The PCA outputs are the percentages of variation accounted for by the main components, correlations between the five parameters and PCA components, and scores of the 120 fruits on the components. Parameters were displayed on the planes of the PCA components by means of points whose coordinates are correlations with components. Cosines of angles between vectors passing



Fig. 3. Distances between absolute growth rate of fruits given in Table 2.

Table 2. Estimated parameters for nine fruits, among the 120 harvested, and their scores on the two first PCA components for cumulated growth and absolute growth rate.

					Scores				
			Parameters	5	Cumulative		Absolute growth		
Fruit	(mm)	$(\text{day}^{-1})$	$P_{3}$ (mm)	$P_4$ (day <sup>-1</sup> )	$P_5$ (days)	PC <sub>1</sub>	PC <sub>2</sub>	PC <sub>1</sub>	PC <sub>2</sub>
1	36.4	0.03	12.9	0.201	66.1	9.2	- 32.3	- 1.94	0.23
2	16.4	0.08	22.5	0.082	65.5	-62.7	4.2	- 2.42	- 1.99
3	21.1	0.05	52.8	0.068	83.9	-1.6	43.1	4.56	- 1.00
4	26.6	0.06	61.3	0.086	79.2	81.6	0.5	4.47	0.73
5	29.7	0.04	32.0	0.170	73.1	15.5	3.8	1.15	0.60
6	27.6	0.05	30.9	0.137	75.1	-7.4	8.4	1.14	- 0.53
7	22.8	0.05	30.4	0.143	68.8	-13.6	11.4	- 0.24	0.09
8	29.3	0.05	24.5	0.233	60.8	37.6	-21.4	- 1.78	2.49
9	28.8	0.05	6.1	0.225	54.9	-10.59	-34.89	-4.89	1.13

through the origin and the points of the parameters were thus equivalent to correlations. The vectors having a length close to 1 were well correlated with the plane of the two components and were those most important for interpreting the plane. We plotted the scores of fruits on successive PCA components to see whether or not they were grouped within different subpopulations.

The highest ranking PCA factors summarized the structure of the population of growth curves. Consequently, the four treatments were compared on factorial planes using a 95% confidence region for the mean based on PCA score values (Scheffé, 1959). Sources and magnitudes of variation in fruit growth between and within peach trees were also identified. Assuming no treatment effect for each of the highest ranking components, the total sum of squares  $SS_{tot}$  of the fruit scores was divided into SS's for each source of variation, i.e.,  $SS_{tot} = SS_{tree} + SS_{shoot}$  $+ SS_{fruit}$  where:  $SS_{tot} = \sum_{iik} (y_{ijk} - \overline{y}_{...})^2$ ;  $SS_{tree} = \sum_{i=1}^{2} n_i(\overline{y}_{i..} -$   $\overline{\mathbf{y}}_{...}$ ;  $SS_{shoot} = \sum_{ii} n_{ij}(\overline{\mathbf{y}}_{ij.} - \overline{\mathbf{y}}_{i...})^2$ ;  $SS_{fruit} = \sum_{ii} \sum_{k=1}^{i} (\mathbf{y}_{ijk} - \overline{\mathbf{y}}_{ij.})^2$ ; and  $\mathbf{y}_{ijk}$  = score of fruit k on shoot j of tree i;  $\overline{\mathbf{y}}_{...}$  = grand mean  $\overline{\mathbf{y}}_{i..}$  = mean of tree i;  $\overline{\mathbf{y}}_{ij.}$  = mean of shoot j of tree i;  $n_i$ is the number of fruit on tree i;  $n_{ij}$  is the number of fruit on shoot j of tree i. The contribution of each source of variation (a) is  $SS_{a}/SS_{tot}$ .

## **Results and Discussion**

*Verification* of *statistical assumptions*. The growth curve model explained 98.2% to 99.9% of the variance in the data. The residual SD was always lower than 2.5 mm. Thus, the splitting of individual growth curves into two parts was satisfactory. This result agreed with those of Baker and Davis (1951) and of Dejong and Goudriaan (1989) for mean growth curves of various cultivars. The median of the error E in the population was low for the cumulated growth (0.03) and fairly high for the absolute



Fig. 4. PCA on the cumulated growth: (A) Scores of fruit on the first two components. Digits represent the number of fruit in Table 2. (B) Correlation plot of parameters.



Fig. 5. PCA on the absolute growth rate: (A) Scores of fruit on the first two components. Digits represent the number of fruit in Table 2. (B) Correlation plot of parameters.

growth rate (0.16). Thus, PCA results for the absolute growth rate must only be considered as trends. The rates of the variance of the estimation of parameters by the variance of parameters within the population of fruits were low (0.03 to 0.4). Hence, the distance between growth curves could be computed using the Houllier (1987) method.

Comparison of peach growth curves. The first two components of both PCAs on cumulated growth and absolute growth rates accounted for the bulk of the data variance (91% and 92%, respectively). Fruit were not grouped into subpopulations on  $PC_1 \times PC_2$  PCA planes (Figs. 4 and 5). The first component  $PC_1$  of the PCA on cumulated growth (69% of the data variance) was a gradient of increasing cumulated growth during the first and the second phase of growth, respectively,  $p_1$  and  $p_3$ . The second component  $PC_2$  (23% of the data variance) differentiated between fruit of high cumulated first-phase growth  $(p_1)$  to fruit of high cumulated second-phase growth  $(p_3)$ . Fruit that grew much during the second phase had the latest date of maximal absolute growth  $p_5$  and the lowest relative growth rate  $p_4$  at this date (Fig. 4). To illustrate this, nine fruits, whose estimated parameters and score values are presented in Table 2, were chosen in the plane and some of their growth curves plotted in Fig. 2. The fruit pattern on the first plane of the PCA on absolute growth rates was different from those of the previous analysis (Fig. 5). The first component  $PC_1$  (78% of the data variance) was a gradient of increasing date of maximal absolute growth rate  $p_5$  and cumulated second-phase growth  $p_3$ . The second component  $PC_2$  (13% of the data variance) differentiated between

fruit of high relative second-phase growth rate  $p_4$  to fruit of high relative growth rate  $p_2$  and low cumulated growth  $p_1$  during the first phase (Fig. 5). An illustration is also given in Fig. 3.

To sum up, fruit were characterized first, according to cumulated growth during the two growth phases and the date of maximal absolute growth, and second, according to cumulated growth and relative growth rates during each phase. We did not find any relationship between  $p_1$  and  $p_3$  from the factorial planes. This fact showed that growth during the second phase was uncorrelated with the growth during the first phase, and hence disagrees with the results of Davis and Davis (1948) and Batjer and Westwood (1958). These authors studied orchards of optimal horticultural care. Our horticultural conditions were not optimal because no fertilizer was applied since the trees had been planted. Under such conditions, relationships between early and late growth of fruit could be very weak because fruit growth might be limited by carbohydrate supply during the second phase of growth.

Effect of fruit count per shoot and of leaf : fruit ratio. We used the  $PC_1 \times PC_2$  planes of two previous analyses to study the effect of fruit count and of leaf : fruit ratio on fruit growth (Fig. 6). The treatments had no significant effect on fruit growth since confidence regions of mean scores were almost the same on each factorial plane. Growth variability within treatments was high. Whereas these results agreed with those of Hansen and Christensen (1974) and Hansen (1977), who found no difference in carbohydrate supply to fruit when fruit count per shoot varied considerably within the tree, they differed from



Fig. 6. Plot of fruit scores labeled with treatment number (1-4) on PCA planes: (A) Cumulated growth; (B) absolute growth rate. 95% confidence region of each treatment is drawn.

those involving girdled limbs where peach growth was reported to increase with the leaf : fruit ratio (Jones, 1932; Weinberger, 1931). Three hypotheses could explain these differences: 1) in our study, leaf count could have been large enough to allow maximal fruit growth even under the low leaf : fruit ratio treatment; 2) the leaves of fruiting shoots of low leaf : fruit ratio might have exhibited greater photosynthesis, since this is stimulated by fruit growth (Chalmers et al., 1975; Crews et al., 1975); or 3) the fruits on shoots of low leaf : fruit ratio could have been supplied by assimilates from other parts of the tree, as reported by Hansen and Christensen (1974) and Hansen (1977), which is not possible for girdled limbs. Moreover, the low fruit load of the remainder of the tree could favor assimilate transport toward the shoots studied.

Variability of growth between and within trees. For each of the PCAs, differences among fruits within shoots accounted for more than half of the total variation. Differences among trees and among shoots were equivalent (Table 3). Thus, as shown in Fig. 7, fruits borne by the same shoot could have either high or low cumulated growth (fruits 2 and 7 of the same shoot, respectively) or grow more noticeably during the first or second growth phase (fruits 3 and 5 of the same shoot, respectively). Jackson (1966) and Hansen (1982) noticed this high growth variability within the tree. Several factors could explain this variability: time of bloom of individual flowers (Sullivan, 1965), competition between fruits (Lai et al., 1990), local differences in leaf : fruit ratio, or in fruit exposure (Marini et al., 1991).

In conclusion, the proposed approach is of value for describing growth variation within large populations of fruit by means of biologically meaningful parameters. According to the biological aims involved, other growth criteria, such as relative

Table 3. Sum of squares along PCA components (in percentage of the total sum  $SS_{tot}$ ) partitioned according to each source of variation.

	Cumulated	l growth	Absolute growth rate		
Organism	$PC_1$	$PC_1$	$PC_1$	$PC_2$	
Trees	26.6	23.9	9.6	29.0	
Shoots	19.9	13.5	12.1	17.6	
Fruits	53.5	62.6	78.3	53.4	



Fig. 7. Variability of growth within a shoot on the first PCA plane on cumulated growth. Digits represent the eight fruits on that shoot and points the other fruits.

growth rate, for example, could be studied by this method. The main limitations to the proposed approach lie in the ascertaining of the statistical assumptions concerning the model's fit and the creation of matrices. When this is insufficient, as was the case for absolute growth rate in our study, the results of the analysis can only show the main trends of the data structure.

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