A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth

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Summary A virtual fruit model simulating seasonal changes in several peach (\textit{Prunus persica} (L.) Batsch) fruit quality traits during the final growth stage is presented. The quality traits considered are fruit size, the proportion of total fruit mass consisting of fruit flesh, dry matter content of the flesh and the concentrations of sucrose, glucose, fructose and sorbitol in the flesh, which are used to calculate a sweetness index. The virtual peach fruit model was developed by adapting and integrating three existing process-based models describing fruit dry mass growth, fruit fresh mass growth and sugar accumulation in the flesh into one complex system. Data sets of peach fruit growth and quality obtained from one field site over several years were used to estimate parameters and evaluate the virtual peach fruit model. Output from the model showed good agreement with the field data. Insight into the complex nature of the virtual peach fruit model, i.e., its ability to show emergent properties, was accomplished by conducting a series of theoretical experiments. The virtual peach fruit model was shown to be sensitive to management and environmental factors (leaf: fruit ratio, stem water potential and, to a lesser extent, weather). Its ability to generate simple laws relating to physiological variables and quality parameters was also demonstrated. Finally, the virtual peach fruit model was able to reveal complex behaviors resulting from changes in water potentials or leaf: fruit ratios over time.

Keywords: fructose, glucose, mass, sorbitol, sucrose, sugar concentration, system, theoretical experiment.

Introduction

In recent years, fruit quality has become an increasingly important aspect of fruit production. For example, in Europe, the new market organization enjoins farmers to form producer organizations whose goal is to improve fruit quality. Research efforts directed toward understanding the effects of climate and management techniques on fruit quality are needed, and mathematical models are useful frameworks for these research efforts (Sansavini 1997). Fruit quality, even when reduced to organoleptic qualities (such as sweetness or acidity) that meet consumer demand, is a multi-criterion concept. Each quality trait is the result of a complex chain of biological processes that depend on environmental conditions. These processes are interrelated (e.g., sugar metabolism depends on carbon fluxes) and their effects on quality traits may be opposite (e.g., enhancing water fluxes into fruit increases fruit size but decreases sugar concentration; Génard and Lescourret 2004). Clearly, a useful fruit quality model must take into account several quality traits, the underlying processes and their interactions.

However, following the pioneering work of C.T. de Wit (see van Ittersum et al. 2003), most process-based fruit models have focused on carbon relationships leading to predictions of fruit growth in dry mass. Such photosynthesis-driven models have been developed for apples (Baumgaertner et al. 1984, Seem et al. 1986), grapes (Gutierrez et al. 1985), kiwifruit (Buwalda 1991), olives (Abdel-Razik 1989), peaches (Grossman and De Jong 1994) and tomatoes (Heuvelink and Bertin 1994). Some models have dealt with nitrogen content, representing nitrogen and carbon dynamics on a similar conceptual basis (sink-driven assimilation and allocation using priority rules; Wermelinger et al. 1991). Researchers have modeled water accumulation in fruit, considering water uptake and transpiration per unit fruit area as constant (Lee 1990) or variable (Génard and Huguet 1996). In a more mechanistic work applied to tomatoes, the difference between water potentials in the stem and the fruit was assumed to be the driving force of water import rate (Bussières 1994). Another tomato water model focused on the role of pedicel resistance and calyx transpiration (Bussières 2002). A few models of fruit metabolism describing synthesis and degradation processes have been designed for sugar (Génard and Souty 1996) and citric acid accumulation (Lobit et al. 2003). However, few models consider several processes together (except Bussières 1993, 1995 and Fishman and Génard 1998, with interrelated C and water transports).

In this paper, we propose a modeling approach that can simultaneously simulate changes in several quality traits throughout the final stage of fruit growth, using the example of peach (\textit{Prunus persica} (L.) Batsch). These traits include: fruit size, the most important commercial criterion for growers; the proportion of the total mass consisting of fruit flesh, which is important for the consumer; dry matter content of the flesh; and flesh concentrations of various sugars. Our threefold approach...
was based on the existence of specialized models (i.e., devoted to categories of traits) already published, validated and used. First, we integrated these models into a virtual peach fruit model to simulate the interactions between processes and their consequences on quality. Second, we validated the approach by comparing model predictions with data collected over different years and growing conditions. Third, we studied the emerging behavior of the virtual peach fruit model as a product of its complexity. By emerging behavior we mean, in the sense of systems theory, properties that cannot be reduced to those of the components (i.e., to the basic knowledge incorporated into the models). Three questions structured the study of emergent behavior: (1) To what extent is the virtual peach fruit model sensitive to environmental factors? (2) Is it able to generate simple and general laws? (3) Is it able to produce complex behaviors? To answer these questions, we performed theoretical experiments with the virtual peach fruit model, involving typical environmental factors of fruit crops. The factors were: weather, which cannot be controlled and is nowadays subjected to intensive modeling research (e.g., modeling projected effects of global change (Tubiello et al. 2002, Wolf 2002)); plant water status variables resulting from the regime of water uptake, which can be partially controlled; and leaf:fruit ratio, which can be strongly controlled by thinning practices.

Description of the virtual peach fruit model

The virtual peach fruit model (Figure 1) represents the quality buildup of a “mean” fruit on the fruit-bearing stem, which is the basic production unit for peach growers. This unit is a 1-year-old stem (20–50 cm long) that bears fruit and new shoots. The virtual peach fruit model runs on a daily time step. Peach fruit development occurs in three stages, with active growth during the first and third stages and stone hardening during the second (plateau) stage. The virtual peach fruit model concerns the third stage corresponding to the enlargement of flesh cells and includes 80% of fruit growth. The virtual peach fruit model is a combination of three sub-models of which one describes the management of carbon, one the management of water and one the buildup of sugars. The sub-models, their adaptations and connections are described briefly below.

Carbon sub-model

The carbon sub-model has been described by Lescourret et al. (1998). It has been successfully tested with data sets from several field sites and years (Génard et al. 1998), and used to analyze fruit growth from different viewpoints (Génard et al. 1998, Quilot et al. 2002, Walcroft et al. 2004).

The fruit-bearing stem is divided into three compartments: fruits, 1-year-old stem and leafy shoots, considering carbon reserves (except in fruit) and dry mass in each. The pool of carbon assimilates available daily is the assimilation of leaves plus that mobilized from either local reserves, or from other parts of the tree (Walcroft et al. 2004). Here we consider only local assimilates. Light-saturated leaf photosynthesis, an important component of leaf photosynthesis, is possibly changed by: (1) a feedback inhibition through the leaf storage reserves; and (2) leaf water potential, as detailed by Ben Mimoun et al. (1999). Total daily leaf photosynthesis is the sum of hourly photosynthesis by sunlit and shaded leaves. Sunlit and shaded leaf areas are computed with coefficients describing the between-shoot shadow (originating from the foliage of the surrounding shoots) and the within-shoot shadow (mutual shadow of leaves within a shoot), respectively (input data). Such coefficients are assumed to follow a simple seasonal pattern of variation and may be estimated using gap fractions derived from fisheye photographs. Carbon assimilation by fruits is considered on a similar basis, with a temporal component accounting for the seasonal decline in fruit photosynthesis. If required, reserves are mobilized first from the leafy shoot, then from the 1-year-old stem. It is assumed that a fixed fraction of reserves can be mobilized each day.
Carbon is allocated according to organ demands (as modified by the effects of temperature and of dry mass already accumulated) and priority rules. Maintenance respiration costs are given first priority, with vegetative and reproductive growth given second and third priority, respectively. The assimilates unused for maintenance and growth accumulate in the reserve pools of leafy shoots and 1-year-old stem.

Daily carbon demand, \( D \), for fruit growth is subjected to a new parameterization in the present work. An important component of the sugar sub-model (see next section) requires taking account of the beginning and end of fruit maturation, which can be equal to zero depending on the compartment, representing the carbon flows from the phloem and the carbon loss by respiration, respectively; \( k_{ij} \) is a function of parameters \( \theta \); and variables \( x \) describing the relative rate of transformation of sugar \( i \) into sugar \( j \). According to the equations given by Génard et al. (2003), the relative rate of sucrose transformation into glucose and fructose depends on phenological time (day after full bloom) through an exponential equation; the relative rates of sorbitol transformation into fructose or glucose are constants; and the relative rate of transformation of either glucose or fructose into compounds other than sugars is modeled as being linearly related to the relative growth rate of flesh dry mass.

### Water sub-model

The water sub-model is an adaptation of the biophysical model of fruit growth developed by Fishman and Génard (1998) and revised by Lescourret et al. (2001). The time course of water mass in the fruit flesh is calculated assuming that water enters the fruit flesh from xylem and phloem and is lost through transpiration. The flow of solution from xylem or phloem to the fruit cells follows a general law:

\[
U = AL(P - P_i - \sigma(p - p_i))
\]

where “\( i \)” refers to fruit variables, \( A \) is the external surface area of the vascular network assumed to be proportional to fruit area \( A_f (A = a A_f) \), where \( a \) is a non-dimensional coefficient of proportionality, \( L \) is the hydraulic conductivity coefficient of vascular network membranes, \( P \) and \( p \) are the hydrostatic and osmotic pressures, respectively, and \( \sigma \) is a measure of impermeability of the membrane to solutes. In the case of xylem, water must cross the plasma membrane of cells, for which \( \sigma \) is close to 1 (Nobel 1974, Murphy and Smith 1994). Water can enter fruit cells from phloem through plasmodesmata (Patrick and Offler 1996). However, most plasmodesmata are closed, relatively high concentrations (Patrick and Offler 1996, Patrick et al. 1997). Thus, \( \sigma \) was assumed to be close to one for both xylem and phloem.

The fruit osmotic pressure induced by sugars is calculated by means of the sugar sub-model outputs. The hydrostatic pressure of the fruit flesh is calculated by solving the Lockhart equation describing the growth in volume, \( V \), of the fruit flesh (Lockhart 1965) as a function of pressure and current fresh mass:

\[
\frac{dV}{dt} = \begin{cases} 
V_\varphi(P_i - Y), & \text{if } P_i > Y \\
0, & \text{if } P_i \leq Y
\end{cases}
\]

where \( \varphi \) is extensibility of the cell walls and \( Y \) is the yield threshold value that the hydrostatic pressure of the fruit flesh has to exceed before irreversible expansion occurs. Assuming that the change in fruit flesh volume mainly results from water balance, it can also be calculated from Equation 6 as:
where “x” and “p” refer to xylem and phloem, $D_w$ is water density and $T_f$ is fruit transpiration rate. Under the condition of steady irreversible growth, Equations 5 and 6 must be equal. Setting them equal, and inserting the flux from Equation 4, the resulting equations for $P_f$ can be solved. If the environmental conditions lead to low $P_f$ values, the cell wall stresses are relieved and $P_f$ is assumed to stay close to zero (Fishman and Génard 1998). In this case, Equation 5 is no longer valid and the change in fruit flesh volume is calculated from Equation 6. This change may be negative, so that the model takes into account that water can be exported from the fruit into other plant organs as shown by Greenspan et al. (1996).

The initial model ran on an hourly basis, considering the hourly variations in stem water potential, temperature and air humidity, the last two variables being implicated in fruit transpiration. When the virtual peach fruit model is run on a daily basis, hourly variation is not considered. For various water conditions, we compared model outputs using series of either hourly values of the three input variables, or daily values each corresponding to hourly (24) values averaged per day. With a slight variation in parameter $a$ (Equation 4) (see Materials and methods), we obtained similar fresh mass curves (mean absolute difference about 2–4%). Averaged over a day, the osmotic pressures and the hydrostatic pressures greater than $Y$ (Equation 5) were also similar (data not shown). Thus, the mean daily values of stem water potential, temperature and air humidity proved adequate for predicting the daily fruit water balance.

Determination of stone fresh mass, $M_{st}$, was required to compute the part of total mass consisting of flesh. It used stone dry mass calculated by the carbon sub-model, $DM_{st}$, and the following empirical relationship:

\[ M_{st} = \text{stone}_1 \times DM_{st} \times \text{stone}_2 \]  

where $\text{stone}_1$ and $\text{stone}_2$ are parameters.

The quality traits we considered were derived from the intermediate outputs of the combined model (flesh and stone dry masses, amounts of sugars and water mass in the fruit flesh, stone fresh mass; Figure 1). A sweetness index (g of equivalent sucrose per 100 g of flesh fresh mass) was computed as a linear combination of sugar concentrations, with the sweetness ratings of each sugar (Kulp et al. 1991) as coefficients.

Materials and methods

Calibrating and testing the virtual peach fruit model

Three experiments were performed in 1993, 1996 and 1997 on peach trees of the late maturing cv. ‘Suncrest/GF 677’ planted in 1982 at the INRA Centre of Avignon, France (43.9° N, 4.8° E). Trees were goblet-trained and received routine horticultural care, including non-limiting irrigation. Three leaf: fruit ratios (6, 18, 30 leaves per fruit) in 1993 and 1996, and two leaf:fruit ratios (10, 30 leaves per fruit) in 1997 were applied to 240 (1993, 1996) or 120 (1997) fruit-bearing stems isolated from the rest of the tree by girdling, on 36–45 trees between mid-May and early June, depending on the year. Vegetative growth was prevented by removing the shoot tip. For every year and treatment, five replicates (made up of fruit from one to two similar shoots) were harvested weekly until fruit maturation. Each measure comprised fruit fresh mass, the fresh and dry masses of the stone, the dry matter content of flesh (evaluated after drying at 70°C for 72 h), and the concentrations of the four sugars (% of flesh fresh mass). The sugars were measured by high performance liquid chromatography (HPLC) (see Génard and Souty 1996 and Génard et al. 2003). The measurements obtained for a replicate were averaged. The corresponding data, which have been published by Génard et al. (2003), were used to: (1) estimate parameter $a$ implicated in water inputs (Equation 4) and parameters needed to compute the sharing of carbon between the fruit flesh and the stone and stone fresh mass (Equations 2 and 7); (2) test the goodness-of-fit of the virtual peach fruit model; and (3) evaluate the predictive quality of the peach fruit model.

During 1996, leafy shoots and 1-year-old stems were harvested at dawn (five replicates per treatment and harvest date), and analyzed to evaluate the amount of carbon reserves per unit mass. Soluble sugars and starch were determined as described by Gomez et al. (2002) and Jordan and Habib (1996), respectively. The carbon reserve data were used to estimate parameters of reserve mobilization in the carbon sub-model (see below).

Data from various experiments conducted from 1991 to 1997 on cv. ‘Suncrest’ at the INRA Centres of Avignon or Gotheron (120 km north of Avignon) were combined to create a database of regular measurements of fruit growth in dry mass (861 masses and 127 dates) in non-limiting carbon conditions (30 leaves per fruit or more). From this database, parameters of potential fruit growth in dry mass were estimated (see below). Data obtained in 1991 also comprised stone dry and fresh masses; they were added to data of the same type obtained in 1993, 1996 and 1997 to estimate the parameters of Equations 2 and 7.

Inputs of the virtual peach fruit model

Global radiation, temperature and relative humidity data (Figure 1) were collected by INRA weather stations close to the experimental fields. Because the experimental trees were well-watered, a daily value of ~0.45 MPa was taken for stem water potential based on the mean of hourly default values for well-watered peach trees used by Fishman and Génard (1998), from which the water sub-model originates. Between- and within-shoot shadow coefficients to compute photosynthesis (Figure 1) were mean values extracted from databases constituted for cv. ‘Suncrest’ on the basis of fisheye photographs (see carbon sub-model description). The 1996 data were used to initialize the stem and shoot variables for every simulation. For simulations corresponding to given experimental conditions (year, leaf:fruit ratio), the fruit variables were initialized by averaging the data observed in these conditions on the first date of measurement.
Parameter estimation

The original values of most of the parameters of the sub-models were taken from Fishman and Génard (1998), Lescourret et al. (1998, 2001) and Génard et al. (2003), with the following exceptions.

Parameters of reserve mobilization in the carbon sub-model, \( r_4 \) (leafy shoot mobile fraction of reserves) and \( r_5 \) (1-year-old stem mobile fraction of reserves) were taken from the literature in the original carbon sub-model (Lescourret et al. 1998). Here they were estimated with the 1996 reserve data, by minimizing a weighted sum of the MSE (mean squared error, i.e., mean squared difference between observed and model values) for each of the six combinations of reserve compartment (stem or leaf) and leaf:fruit ratio (6, 18 or 30). The MSE for each combination was weighted by the inverse of the variance of the corresponding data. The estimated values were \( r_4 = 2.6 \times 10^{-2} \) day\(^{-1} \) and \( r_5 = 5 \times 10^{-4} \) day\(^{-1} \) (\( n = 56 \)).

A preliminary estimation of parameters of potential fruit growth in dry mass, \( dd_{\text{max}} \), \( RGR_{\text{ini}} \) and \( DM_{\text{max}} \) (Equation 1) was presented in Lescourret et al. (1998). However, initial tests of the virtual peach fruit model showed that it was necessary to revise these estimates. The \( dd_{\text{max}} \) was estimated as the maximal value observed in the previously mentioned database (1800 dd). The other parameters were estimated by nonlinear least squares regression, using 90 masses for 31 dates corresponding to the higher values in the data set (90% quantile at each date). Estimated values were \( dd_{\text{max}} = 839 \) dd (SE = 270 dd), \( RGR_{\text{ini}} = 4.04 \times 10^{-3} \) dd\(^{-1} \) (SE = 1.64 \times 10^{-4} \) dd\(^{-1} \) ) and \( DM_{\text{max}} = 59.22 \) g (SE = 10.71 g, \( n = 90 \)).

Parameters \( \text{share}_1 \) and \( \text{share}_2 \) (Equation 2), and \( \text{stone}_1 \) and \( \text{stone}_2 \) (Equation 7) were specific to the combined model. They were estimated by nonlinear or linear regressions. Estimated values were \( \text{share}_1 = 5.80 \) (SE = 0.089 g), \( \text{share}_2 = 0.10 \) (dimensionless, SE = 0.035) and \( \text{stone}_2 = 3.82 \) g (SE = 0.15 g, \( n = 677 \)).

Parameter \( \alpha \) in the water sub-model (Equation 4) had been subjected to a calibration procedure in the original biophysical model of fruit growth (Fishman and Génard 1998). Therefore, we reestimated it by minimizing the sum of the MSE over the eight available data sets (combinations of year and leaf:fruit ratio, with 3 years and two to three leaf:fruit ratios). The target of this calibration was the dry matter content of the flesh. The estimated value was \( 2.66 \times 10^{-2} \) (dimensionless, SE = 5.7 \times 10^{-4}, \( n = 391 \)).

Goodness-of-fit and predictive quality of the virtual peach fruit model

To test the goodness of fit of the virtual peach fruit model, the relative root mean squared error (RRMSE) (Kobayashi and Us Salam 2000) was calculated separately for each of the eight combinations of year \( \times \) leaf:fruit ratio and each of the quality traits as:

\[
\frac{1}{\overline{y}} \left( \sum_{i=1}^{N} n_i \left( \frac{y_i - \overline{y}}{\overline{y}} \right)^2 \right)^{1/2}
\]

where \( N \) is the number of dates over the growing period, \( n_i \) is the number of fruit-bearing stems measured at date \( i \), \( y_i \) is the value of the quality trait at date \( i \) calculated by the model, \( \overline{y} \) is the average of values for the “mean” fruits corresponding to \( n_i \) shoots, and \( \overline{Y} \) is the mean of all observed values.

The predictive quality of the virtual peach fruit model, which evaluates the validity of the model outside its range of development, was computed for each fruit quality trait. The criterion was a relative root mean squared error of prediction (RRMSEP). The classical MSE (mean squared error of prediction) was first computed based on the eight experimental data sets (year \( \times \) leaf:fruit ratio combinations), by cross-validation (cf. Batchelor et al. 1994, Wallach et al. 2001). Cross-validation is a common approach to estimating prediction error. It is a more objective alternative to splitting the data, using part for adjustment and part for evaluation, because the way data are split influences both estimation and prediction error (Wallach et al. 2001). The principles of cross-validation are as follows (Wallach et al. 2001). Two data sets are made: one set contains a single situation (the target situation, in our case a single combination of year and leaf:fruit ratio), and the other, all the data independent of the target situation (in our case, not from the same year). Parameters are fitted using the second data set. In our case, just five parameters were fitted in this way because their estimation was largely based on the eight situations: \( \text{share}_1, \text{share}_2, \text{stone}_1, \text{stone}_2 \) and \( \alpha \) (Equations 2, 4 and 7). The error of the resulting model is calculated based on the target situation. The procedure is repeated using every situation in turn as the target situation, and averaging the errors over all the target situations gives an estimate of the prediction error.

Design of theoretical experiments

In the first theoretical experiment, three factors were varied together: weather, leaf:fruit ratio and stem water potential. For weather, 11 data series extracted from the INRA climatic database (years 1992 to 2002 at Avignon) were analyzed by principal component analysis followed by hierarchical clustering on the main components, yielding two main classes. Two contrasting climatic years representative of these classes (1997 and 1998) were chosen as levels for the “weather” factor. Compared with 1997, 1998 was on average (based on daily values) 2 °C warmer, received about 200 µmol m\(^{-2}\) s\(^{-1}\) more global radiation (daily averaged hourly photosynthetic photon flux), and was less humid (mean relative humidity of 0.52 compared with 0.68 for 1998). For leaf:fruit ratio, the three values chosen were 6, 18 and 30 leaves per fruit. Stem water potential daily values (see water sub-model description) corresponded to normal watering (–0.45 MPa) or water stress. In the latter case, different values were attributed to the three leaf:fruit ratios (–0.65, –0.79 and –0.92 MPa for 30, 18 and 6 leaves per fruit, respectively) because stem water potential varies according to crop load (Berman and DeJong 1996). These values were calculated by averaging hourly values proposed by Fishman and Génard (1998) for these water and crop load conditions. The simulations (one per combination of factor levels) took place from 81 to 139 days after bloom, each factor level was kept constant during the simulation period. The sensitivity of the virtual peach fruit model to factors was
assessed by contributions to the sum-of-squares resulting from variance analysis, considering the main effects of the three factors plus time as a linear numerical covariate.

In the second theoretical experiment, four time-scenarios of conditions of stem water potential were studied. In two scenarios, the water conditions were kept constant throughout the simulation period (81–139 days after bloom). They corresponded to conditions of normal watering or water deficit (−0.45 and −0.79 MPa as daily values for stem water potential, respectively). The two other scenarios, which used the same values of stem water potential, were a period of normal watering followed by a period of water deficit of the same duration, and conversely a period of water deficit followed by a period of normal watering of the same duration. Weather was that of year 1997, and leaf:fruit ratio was 18 leaves per fruit.

In the third theoretical experiment, four time-scenarios of leaf:fruit ratio were studied. In two scenarios, the leaf:fruit ratio was kept constant throughout the simulation period (81–139 days after bloom): 30 and 6 leaves per fruit, respectively. In two other scenarios, the simulation period was split into two equal parts, with either 30, then 6 leaves per fruit (which may be obtained by leaf removal), or 6, then 30 leaves per fruit (which may be obtained by fruit removal). Weather was that of year 1997 and daily stem water potential was −0.45 MPa.

The three experimental designs were not intended to represent real situations—keeping water stress constant or setting up time-scenarios of water or leaf:fruit ratio such as those described here would be difficult if not impossible. The three experimental designs were intended solely as a theoretical framework to explore the behavior of a modeled system.

All statistical analyses were performed with the S-plus statistical package (Version 3.4, release 1 for Sun SPARC, SunOS 5.3: 1996).

Results and discussion

Goodness-of-fit and predictive quality of the virtual peach fruit model

The virtual peach fruit model simulated the order of magnitude and seasonal variations of reserve content for three leaf:fruit ratios (Figure 2) and of quality traits for several leaf:fruit ratios and the 3 years (Figure 3). According to the goodness-of-fit criteria (Table 1), there was good agreement between model and data for the proportion of flesh in the total mass. The agreement was also quite good for fruit fresh mass and dry matter content of the flesh. Larger model errors were found for flesh concentrations of sugars and the sweetness index. The largest relative errors were for sorbitol, and were partly associated with the low concentrations of this compound.

The predictive quality of the virtual peach fruit model was good: the RRMSEP values, which ranged from 0.03 to 0.44 (in the case of sorbitol concentration), were close to the mean of RRMSE values and followed the same hierarchy (Table 1).

To what extent is the virtual peach fruit model sensitive to environmental factors?

The first theoretical experiment, which involved the factors weather, leaf:fruit ratio and stem water potential, with time as a covariate, was intended to answer this question. Here we restrict examination of the virtual peach fruit model response to some important physiological and quality variables. The physiological variables were: the photosynthesis rate per unit leaf area that depicts carbon source activity; the fruit carbon demand per fruit that depicts carbon sink activity; the fruit hydrostatic pressure that determines fruit growth in fresh mass according to Lockhart equation implemented in the water sub-model; and the relative rate of synthesis of compounds other than sugars from fructose and glucose that is indicative of the intensity of sugar metabolism in the fruit. The quality traits were fruit fresh mass, the proportion of flesh in the total mass, the dry matter content of the flesh, and the sweetness index.

The range of quality traits over the treatments was wide: at the end of the simulation, values ranged from 67 to 182 g for fresh mass, 0.86 to 0.94 for the proportion of flesh, 0.11 to 0.18 for dry matter content of the flesh, and 5.5 to 10% for the sweetness index. The factor contributions to the total sum-of-squares following analysis of variance are presented in Ta-
Table 2. Some striking points emerge from the results. First, all the variables studied but two (photosynthetic rate and dry matter content of the flesh) are developmentally regulated, so that time (i.e., days after bloom) made a large contribution to their variation. Second, the virtual peach fruit model is clearly sensitive to environmental factors, which accounted together for 26–80% and 8–65% of the total sum-of-squares for quality traits and physiological variables, respectively. However, the effect of weather was unimportant compared with other factors, which is in agreement with the small year effect found in experimental studies on apple (Malus domestica Borkh.) and peach fruit quality (Robinson et al. 1991, Génard et al. 2003).

Leaf:fruit ratio contributed highly to photosynthetic rate and to a lesser extent to fruit demand, and consequently to fruit metabolism, including osmotic potential that was lower for high ratios (data not shown). As a consequence, the mass of water in the fruit, and thus the fresh mass, increased with leaf:fruit ratio, as in the experiment of Berman and DeJong (1996) and the observations of McFadyen et al. (1996). The effects of leaf:fruit ratio on both dry matter content of the flesh and sweetness index were marked for well-irrigated fruits, in accordance with previous experiments (Génard et al. 2003), but almost non-existent in the case of water-stressed plants (data not shown).

Table 1. Goodness-of-fit (RRMSE) and predictive quality (RRMSEP) of the virtual peach fruit model. Abbreviation: DM = dry matter.

<table>
<thead>
<tr>
<th>Quality trait</th>
<th>Mean and range of RRMSE</th>
<th>RRMSEP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh mass</td>
<td>0.14 (0.10–0.20)</td>
<td>0.16</td>
</tr>
<tr>
<td>Proportion of flesh in the total mass</td>
<td>0.016 (2 × 10^{-4}–0.09)</td>
<td>0.03</td>
</tr>
<tr>
<td>DM content of flesh</td>
<td>0.13 (0.09–0.16)</td>
<td>0.13</td>
</tr>
<tr>
<td>Sucrose concentration</td>
<td>0.29 (0.15–0.54)</td>
<td>0.29</td>
</tr>
<tr>
<td>Sorbitol concentration</td>
<td>0.42 (0.28–0.60)</td>
<td>0.44</td>
</tr>
<tr>
<td>Glucose concentration</td>
<td>0.18 (0.07–0.33)</td>
<td>0.20</td>
</tr>
<tr>
<td>Fructose concentration</td>
<td>0.18 (0.08–0.33)</td>
<td>0.22</td>
</tr>
<tr>
<td>Sweetness</td>
<td>0.18 (0.08–0.28)</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Figure 3. Time courses of mean observed (points) and simulated (lines) quality traits for 3 years (from left to right: 1993, 1996, 1997) and different leaf:fruit ratios (6, 10, 18, 30). The observed values are from Génard et al. (2003). Abbreviation: FM = fresh mass.
shown). Accordingly, the contribution of leaf:fruit ratio alone was weak, whereas the contribution of its interaction with stem water potential was greater (11 and 6% for dry matter content and sweetness, respectively). Stem water potential contributed substantially to the dry matter content of the flesh and to the sweetness index. This result is consistent with many experimental findings showing increases in fruit soluble solids or sugar concentrations with water stress (Crisosto et al. 1994, Ginestar and Castel 1996, Yakushiji et al. 1998, Chartzoulakis et al. 1999). Third, the contribution of factors was much less for the physiological variables than for the quality traits. In contrast with quality traits, which are at every time-step the result of a history (e.g., the fruit fresh mass is a cumulated value), the physiological variables are either highly regulated (e.g., hydrostatic pressure) or instantaneous and sensitive to day-to-day variation within a weather series, which did not contribute to the variance analysis.

Can the virtual peach fruit model generate simple, general laws?

To answer this question, we use the results of the first theoretical experiment, where various model inputs varied, to examine relationships between quality traits, between physiological variables, and between both. Considering all the data from the first theoretical experiment, a strong link was found between fruit fresh mass and the proportion of flesh in the total mass, and there was a weaker link between dry matter content of the flesh and the sweetness index (Figure 4). Fruit fresh mass and

<table>
<thead>
<tr>
<th>Explanatory variable (df)</th>
<th>PR</th>
<th>EFD^1</th>
<th>LFD^1</th>
<th>Fruit P &gt; 0.5 MPa^2</th>
<th>Synthesis (other than sugar)</th>
<th>Fruit FM</th>
<th>Proportion of the flesh</th>
<th>DM content of the flesh</th>
<th>Sweetness index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day after bloom (1)</td>
<td>8.10</td>
<td>31.62</td>
<td>21.82</td>
<td>38.04</td>
<td>52.34</td>
<td>62.49</td>
<td>62.48</td>
<td>0.42</td>
<td>28.25</td>
</tr>
<tr>
<td>Leaf:fruit ratio (2)</td>
<td>62.02</td>
<td>11.08</td>
<td>33.39</td>
<td>6.14</td>
<td>23.83</td>
<td>20.74</td>
<td>15.34</td>
<td>0.2</td>
<td>4.47</td>
</tr>
<tr>
<td>Ψ^stem^1 (1)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.68</td>
<td>0</td>
<td>5.90</td>
<td>10.32</td>
<td>68.82</td>
<td>45.26</td>
</tr>
<tr>
<td>Weather (1)</td>
<td>2.82</td>
<td>6.46</td>
<td>0.09</td>
<td>0.05</td>
<td>0.09</td>
<td>0.37</td>
<td>0.40</td>
<td>10.02</td>
<td>8.71</td>
</tr>
<tr>
<td>Residuals (690)</td>
<td>27.06</td>
<td>50.84</td>
<td>44.7</td>
<td>54.09</td>
<td>23.74</td>
<td>10.5</td>
<td>11.46</td>
<td>20.54</td>
<td>13.31</td>
</tr>
</tbody>
</table>

1 For fruit demand, two variance analyses were undertaken because of the bell-shaped response of this variable to DAB: for EFD, DAB ≤ 110; and for LFD, DAB > 110.

2 Only pressures > 0.5 MPa, the threshold value above which fruit growth occurs according to the water sub-model of the virtual peach fruit model (Fishman and Génard 1998), were considered.

Figure 4. Pairwise plots of quality traits in the first experiment performed with the virtual peach fruit model. Each plot gathers data of the 12 combinations of factor levels (three leaf: fruit ratios, two weathers and two stem water potentials). Lines relate data (crosses) simulated each day (simulation period = 81–139 days after bloom) for a given combination of factor levels. Pearson correlations are indicated.
the proportion of flesh were also closely linked within every factor combination leaf:fruit ratio × stem water potential × weather (Pearson correlation = 0.95 ± 0.02), partly because both variables were strongly time-dependent (Table 2). Similarly, a unique relationship between flesh and fruit masses was obtained from experimental data by Léchaudel et al. (2002) on mango fruit (*Mangifera indica* L. cv. ‘Lirfa’), for five leaf:fruit ratio treatments ranging from 10 to 150 leaves per fruit. The second link was approximately linear, with fairly large variation. However, correlations between dry matter content of the flesh and sweetness varied from −0.05 to 0.88 among the factor combinations. The most notable feature of this link is that low dry matter content is never associated with high sweetness index, or high dry matter content with low sweetness index. For the other pairs of quality traits, though correlations could be strong within factor combinations, no clear overall pattern emerged from the data.

Among physiological variables (Figure 5), only two relationships were sufficiently strong to merit mention. A positive link was found between fruit carbon demand per unit leaf area and photosynthetic rate, with a strong increase in photosynthetic rate with fruit carbon demand for demand values less than 10 g C m$^{-2}$, then a slower increase with a plateau at about 5.5 g C m$^{-2}$. This relationship was time independent. It is valid for the conditions of the simulation, i.e., the case where only local assimilates, those of the fruit-bearing stem, are considered (see Materials and methods). A similar curve was observed by Ben Mimoun et al. (1996) in the case of experimental data obtained from fruit-bearing stems isolated from the tree by girdling, corresponding to two peach genotypes, 3 years and 5 to 50 leaves per fruit. The second positive link was a linear relationship between carbon demand per fruit and relative rate of synthesis of compounds other than sugars, the slope of which decreased with days after bloom. A likely explanation for this pattern is that periods of intense fruit demand are marked by the synthesis of new structures such as cell walls, whereas synthesis of new structures diminishes as the fruit approaches maturity (Bouranis and Niavis 1992, Fishman et al. 1993).

Physiological variables, which are instantaneous, were not related directly to quality traits, but to their rate of change per unit time. Significant relationships were found with fruit hydrostatic pressure only (Figure 6). Rates of change of both fruit fresh mass and the proportion of flesh increased with fruit hydrostatic pressure, whereas those of dry matter content of the flesh and sweetness decreased. According to the Lockhart law implemented in the model, small increments in hydrostatic pressure are sufficient to increase the rate of change of flesh mass, so that ratios per unit flesh mass, like dry matter content or sweetness, decrease.

Overall, the virtual peach fruit model suggests that simple and general laws are common. In this investigation, pairwise scatter plots of virtual peach fruit model variables demonstrated relationships in about one third of cases.

*Can the virtual peach fruit model produce complex behavior?*

The second theoretical experiment compared four time-scenarios of stem water potential, denoted here as W (constant normal water conditions), W/S (normal water conditions, then water stress, for two equal periods), S/W (water stress, then normal water conditions, for two equal periods) and S (constant water stress). These scenarios produced a wide range of responses of quality traits (Figure 7). The response to the S/W scenario looked like “compensatory growth” after re-watering, because growth loss during the stress period was fully regained after re-watering. A decrease in sweetness and dry matter content and an increase in the proportion of flesh were consequences of this compensatory growth. According to Trewavas (2003), compensatory growth is a corrective mechanism involving feedback control to achieve a developmental goal. We hypothesized that the virtual peach fruit model mimics such a mechanism based on a “sugar signal,” assuming that the increase in sugar concentration during the stress period (as shown in Figure 7 for the sweetness index) promotes growth after re-watering.

Application of water stress after a period of normal water conditions (W/S) resulted in a sharp slowdown in growth. During the same period, fruit that encountered continuous water stress (S) experienced continuous growth, implying that the S fruit had become adapted to drought compared with the W/S fruit. In real plants, this kind of adaptation has been called a
memory effect (Trewavas 2004). We can relate growth patterns to sugar concentration patterns. Sugar concentration was much higher in S plants than in W/S plants at 110 days after bloom, the beginning of the stress period for W/S. We therefore hypothesized that the high sugar concentration allowed fruit growth under conditions of water deficit.

The third theoretical experiment compared four time-scenarios of leaf:fruit ratios, denoted here as 30 (30 leaves per fruit during the entire simulation period), 30/6 (30, then 6 leaves per fruit, for two equal periods), 6/30 (6, then 30 leaves per fruit, for two equal periods) and 6 (6 leaves per fruit during the entire simulation period). The treatments resulted in contrasting responses of quality traits (Figure 8). During a period of 10 days after changing leaf:fruit ratio, i.e., from 110 to 120 days after bloom, sugar concentration and dry matter content changed markedly, decreasing or increasing in the same direction as leaf:fruit ratio, as shown on Figure 8. In the 30/6 and 6/30 scenarios, the responses of fresh mass and of the proportion of flesh to changing leaf:fruit ratio exhibited time lags of 5–10 days. A possible explanation is that, for the 30/6 scenario, the sugar concentration was high enough to maintain rapid growth for a few days after changing the leaf:fruit ra-
tio, whereas in the 6/30 scenario, the sugar concentration was insufficient to immediately increase fruit growth rate. By 120 days after bloom, the responses of every quality trait to the 30/6 and 6 treatments on the one hand, to the 6/30 and 30 treatments on the other hand, were parallel, suggesting that the rate of change of every quality trait depended only on the current leaf:fruit ratio.

In the second theoretical experiment, the W and S/W treatments and the S and W/S treatments produced similar final results for every quality trait (Figure 7). This suggests that, when simulated fruit growth undergoes several periods with different water conditions, the conditions of the last period are the most important. In the third theoretical experiment, all leaf:fruit scenarios produced different results (Figure 8), suggesting that the entire time course of assimilate supply was important in this particular case.

**Conclusions**

To our knowledge, the virtual peach fruit model is the first model to integrate in a systemic framework knowledge of many interrelated processes, resulting in a complex quality profile and emergent properties that are typical of complex systems. The adaptation to water stress, the compensatory growth, and the inertia to changing carbon supply were behaviors that were not predicted at the model design stage. The model offers various possibilities as a research tool, both for performing theoretical experiments and for helping to understand experimental results when studying the effects of technical scenarios for which there is no literature. We examined relationships between quality traits, between physiological variables and between both and found patterns that did not derive just from the aggregation of modeled basic functions. Moreover, the virtual peach fruit model may help in assessing the relative importance of processes for a given complex function or trait. For example, sugar metabolism is generally considered to be the main process leading to sugar concentration, but this assumption has never been verified. The virtual peach fruit model is a powerful tool for studying the respective contributions of sugar unloading, dilution by water and metabolism.

Virtual plants are being viewed as a novel means to simulate the genetic variability of plant responses to environmental conditions (Tardieu 2003). Combining either gene regulatory networks or quantitative trait loci (QTL) and models (Reymond et al. 2003) are two possible avenues, assuming that a genotype is represented by one parameter set (Tardieu 2003). Analyzing genotypic variation by means of models is a first step, and has been done with the carbon sub-model on a contrasting population of peach genotypes (Quilot et al. 2002). The results show that the main process explaining genotypic fruit growth variations is fruit growth demand, allowing for a restricted subsequent QTL analysis of carbon model parameters. This work is being completed and pursued using the virtual peach fruit model. In addition, incorporating the virtual peach fruit model in a crop model (work in progress) will be of value in simulating the combined effects of changes in climate, pest events changing leaf area or photosynthesis, genotype and technical operations on profiles of quality traits, and will thereby help to improve breeding and crop management processes.

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**Figure 8.** Time courses of four quality traits as predicted by the virtual peach fruit model, under four time scenarios of leaf:fruit ratio (30 = 30 leaves per fruit, 30/6 = 30 then 6 leaves per fruit, 6/30 = 6 then 30 leaves per fruit, 6 = 6 leaves per fruit). The arrow indicates the time when leaf:fruit ratio changes in the 30/6 and 6/30 scenarios.
References


