An intelligent virtual fruit focusing on quality attributes

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An intelligent virtual fruit model focussing on quality attributes

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SUMMARY

A process-based model of fruit quality expressing seasonal changes in several quality attributes of fruit (e.g., size, percentages of flesh, water, and sugar contents) on a fruit-bearing shoot (FBS) is presented as a contribution to the SMARTFRUIT work package in the framework of the EU Project, ISAFRUIT. Virtual experiments carried out on 'Zéphir' peach (*Prunus persica* L. Batsch.) showed that fruit size at thinning had a dominant effect on fruit dry mass and the percentage of flesh, whereas water potential had a large effect on both water content and sweetness. Fruit load always had a moderate or small effect on quality attributes. An effect of assimilate supply from the rest of the tree to the FBS was also shown. Based on a wide range of time schedules of water supply, with alternate humid and dry periods of random length, the virtual fruit model suggested, in the case of the cultivar 'Suncrest', that fruit quality at harvest was essentially explained by the duration and humidity of the last period of the time schedule. Finally, during these experiments, the virtual fruit model behaved like a true system, and showed emerging properties of both theoretical and practical interest. We draw conclusions on the opportunities that such a virtual fruit model offers for genetics, agronomy, and ecology, and discuss prospects for the extension of such "virtual fruit" and its incorporation into a "virtual plant".

In Europe, the fruit supply chain is facing new challenges such as increasing the consumption of fruit from sustainable production systems. Under current European (EU) regulations, marketing organisations are required to improve quality all along the supply chain. Growers, who are key stakeholders in this chain, have to adapt their technical choices to present concerns. Scientists must help in this adaptation and in the design of new cropping systems by proposing tools that can improve the decision-making processes. This is an important objective of the ISAFRUIT project, and especially SMARTFRUIT, a work package aimed at increasing fruit quality by making use of available resources such as water, light, and plant genetic potential, in a smart and sustainable way.

Biological, technical, and economic models are useful as complementary tools to support decision-making in agriculture. Biological models are especially necessary to take into account a wide range of criteria, and to allow for rapid adaptation through evaluation, exploration, and learning (Boiffin *et al*., 2001).

To be able to help growers face unusual situations, any biological model must, in our view, be process-based. Process-based models are more capable of accommodating unusual situations than empirical models that can only be used under the particular range of conditions that were used to develop them. Moreover, only process-based models are able to integrate scientific knowledge from 'omics' studies, or to consider, properly, all biotechnological advances.

In terms of the biological models applied to fruit production, much work remains to be done, as few current models deal with fruit quality. Following the pioneering work of De Wit and Goudriaan (1978), most process-based models that consider fruit have focussed on carbon relationships, leading to predictions of fruit growth in terms of dry weight (DW; Heuvelink and Bertin, 1994). Few models have considered several processes together, even though quality attributes depend on many common and/or antagonistic processes. Clearly, the complexity of the fruit quality profile requires modelling of these underlying processes, and their interactions, and must explicitly consider environmental variables that may be technically driven (such as the leaf-to-fruit ratio), in order to improve our understanding of the effect of technical changes. It is therefore imperative to design an "intelligent" model that can react to unusual growing conditions.

In this paper, we exemplify a multi-criterion, process-based model of fruit quality. This so-called "virtual fruit" was based on the approach of Lescourret and Génard (2005). We present examples of model development and its use to analyse environmental effects. We focus on peach (*Prunus persica* L. Batsch.) and on attributes of interest to both growers and consumers, which are the two endpoints of the fruit supply chain and are thus key targets for ISAFRUIT research. The attributes studied were: fresh weight (FW; g), which determines the price paid to the grower, the percentage of flesh in the fruit (g 100 g^{-1}), which determines the extent of the edible part of the fruit, and water and sugar contents, which determine fruit taste, which is the driving force of consumer satisfaction.

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BRIEF OVERVIEW OF THE MODEL

A peach tree can be considered, from a fruit grower's viewpoint, as a collection of fruit-bearing shoots (FBS). Accordingly, our model represents FBS functions, with a strong focus on the fruit. The model is composed of four existing process-based models that describe the dry weight (DW; g) growth of the different components of the FBS, including the fruit itself, sugar accumulation in the fruit flesh, the growth in fruit FW (g), and fruit surface conductance to water vapour diffusion. The model concerns stage III of fruit growth and runs on a daily basis.

The increase in DW was modelled as the carbon balance of a FBS, according to the supply and demand approach of Lescourret *et al*. (1998). The daily available pool of C-assimilates consisted of leaf assimilation plus C eventually mobilised from reserves, and possibly C from the rest of the tree. The level of C transfer depended on the leaf-to-fruit ratio (i.e., the number of leaves per number of fruit) on both the FBS and the tree (Gibert *et al*., data not shown). Leaf photosynthesis, at the FBS level, may be affected by feedback inhibition caused by leaf C-reserves. Carbon is allocated according to organ demand and priority rules. Maintenance respiration costs, vegetative growth, and reproductive growth have first, second, and third-order priorities, respectively. The C-demand for fruit growth depends strongly on sink size and activity, which means that fruit history plays an important role in fruit C-demand. The latter also depends on developmental stage. The incoming C-flow is shared between the fruit flesh and the endocarp plus seed, according to an equation derived from an empirical relationship between endocarp plus seed DW and total fruit DW. Using the compartmental approach of Génard *et al*. (2003), fruit flesh C is then partitioned into several compounds: four sugars (sucrose, sorbitol, glucose and fructose) in the case of peach. Other components were considered as a whole (starch and structural carbohydrates), and respired CO_2. The rates of change in the amounts of C in the four sugar compounds are described using a set of differential equations based on the "rate law" of chemical kinetics (Chang, 2000), which states that the rate of a reaction is proportional to the concentration of a reactant in the fruit.

According to the biophysical approach of Fishman and Génard (1998), the flow of water into the fruit is driven by differences in the hydrostatic and osmotic pressures between the xylem or phloem, and the fruit. Fruit osmotic pressure induced by sugars is calculated using previous predictions of C compartmentation. The increase in fruit volume is assumed to be proportional to the hydrostatic pressure according to Lockhart (1965). Fruit transpiration is calculated from the conductance of the skin to water vapour, and the difference in vapour pressure between the air and the fruit. The model of Gibert *et al*. (2005) was used to represent fruit surface conductance as the sum of the stomatal, cuticular, and crack conductances.

Inputs into the fruit quality model were weather data (i.e., global radiation, temperature, and relative air humidity), leaf and stem water potentials, and the numbers of leafy shoots and fruit on the stem. The quality attributes considered were fruit FW, the percentage of flesh in the fruit (g 100 g^{-1}), water content, the concentrations of different sugars, and a sweetness index (g sucrose equivalent 100 g^{-1} flesh FW) computed as a linear combination of sugar concentrations, with sweetness ratings for each sugar (Kulp *et al*., 1991) as coefficients.

HIGHLIGHTS OF MODEL DEVELOPMENT AND USE

Analysis of peach fruit dry weight growth

As stated above, an important step in the modelling work was to analyse the C-demand of fruit for growth. To exemplify this analysis, we used the late-maturing cultivar, 'Zéphir' as a case study. We used measurements of fruit growth from trees with low fruit loads corresponding to 89 separate fruit growth curves. Further details of the growing conditions and sampling methods can be found in Gibert *et al*. (2007). Such non-limiting C conditions, under which fruit growth was generally referred to a "potential growth" because fruit demand was satisfied throughout fruit development, are suitable to estimate parameters in the equation describing fruit C-demand. Different equations were tested. A logistic equation was chosen to describe "potential fruit growth" from 700 degree days (°C d) after bloom to harvest (1,800 °C d). The equation used was:

$$DW(t) = \beta \times \frac{DW(t_o)}{1 - e^{(-P2 \times (t - P3))}}$$

where DW was the fruit dry weight (g), and β, P_2 and P_3 were parameters. Time t was in degree days (t_0 = 700 °C d). The product $\beta \times DW(t_0)$ is the maximum DW that a fruit can reach.

The goodness-of-fit of the equation was satisfying. The model was able to predict the variability in growth for low-fruit-load trees by considering only variability in DW at 700 °C d (Figure 1A).

Applying the "potential fruit growth" model directly to fruit on high fruit load trees led to an overestimation of fruit growth (Figure 1B). This showed that the initial DW, which was the only source of variation in the "potential fruit growth" model, could not, alone, explain all of the variation in fruit growth. When included in a global fruit model that explicitly considered C-supply as a limiting driving force, the "potential fruit growth" equation correctly predicted fruit growth on high fruit load trees (Figure 1C).

The virtual fruit model fits well to the quality data

Figure 2 shows the time-course of quality attributes during fruit growth, either monitored directly or simulated by the virtual fruit model, in the case of the mid-season peach cultivar, 'Suncrest'. Peaches were grown on girdled FBS isolated from the rest of the tree, with high or low fruit loads. Further details of the data, and the sampling and analysis procedures can be found in Génard and Souty (1996).

The model accounted for the increase in fruit growth for low-load FBS compared to high-fruit-load FBS. The observations indicated that water contents and the percentage of flesh in the fruit increased over time, and that their levels were higher and lower for high-load than

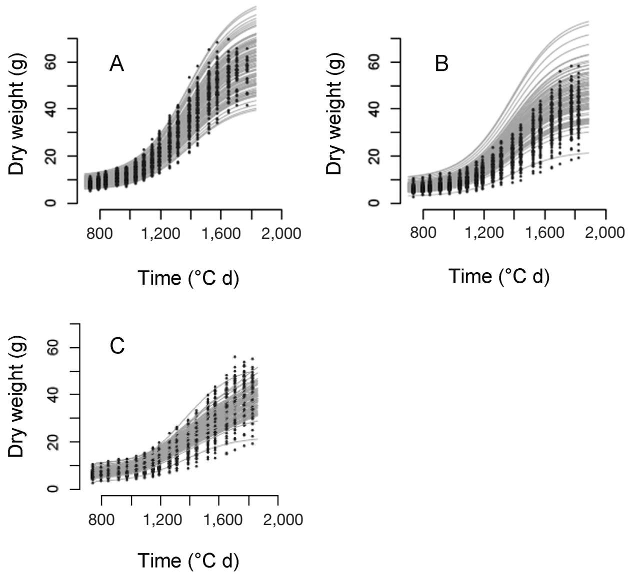

FIG. 1
Fruit growth curves (dry weight in g) of 88 peach fruit ('Zéphir') measured on low fruit load trees in 2004 (Panel A), 89 peach fruits ('Zéphir') measured on high fruit load trees in 2004 (Panel B), 214 peach fruit ('Zéphir') measured on high fruit load trees in 2005 (Panel C). The points are the measurements and the lines are the adjustment using the logistic model (Panel A), predictions with the logistic model (Panel B), and predictions using the virtual fruit model (Panel C).

for low-load FBS, respectively. The model reproduced these unpredictable patterns, which was the first indication of its "intelligence". Figure 2 also demonstrates that the model correctly represented the kinetics of the different sugars and the hierarchy of their levels at harvest, with the highest level for sucrose, followed by glucose, fructose, then sorbitol, as well as the effect of fruit load on sugars, with higher sweetness values for low fruit loads.

Virtual experiments on environmental factors

In the first series of virtual experiments, the virtual fruit model was used to analyse the effect of DW at the fruit thinning stage, fruit load of the FBS, and assimilate supply from the tree, on fruit growth (DW) in the case of 'Zéphir' peach. For the two first factors (indicative of thinning time and intensity, respectively) we used the current range of variations in this cultivar: namely 3 – 8 g for fruit DW at thinning, and one to six for the number of fruit per FBS. For the third factor, assimilates were allowed to be transferred from the tree to the FBS, or not, which mimics girdling at the basis of the stem to suppress phloem flow. The simulations showed large effects of all three factors. The effect of fruit load was much less when the FBS assimilate supply was supplied by the tree (Figure 3).

Assuming that the FBS was supplied by the tree, and using a variance decomposition procedure, the virtual fruit model was used to analyse the effect of fruit DW at the fruit thinning stage, the fruit load of the FBS, and plant water status (indicative of irrigation strategy and depicted by stem water potential), on fruit quality at harvest in 'Zéphir' peach. The ranges of variation in fruit DW at thinning and fruit load per FBS were as stated above. The mean stem water potentials (–0.73 MPa to –0.57 MPa) also corresponded to commonly-used

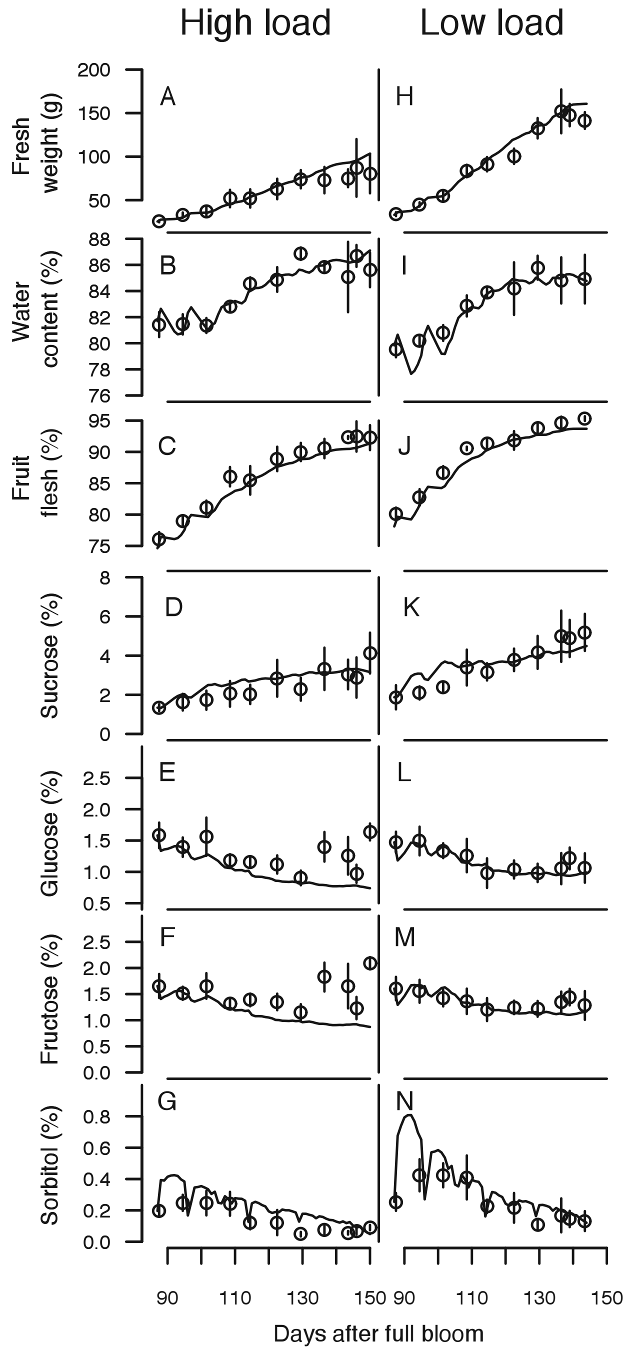

FIG. 2
Time-courses of various quality attributes in peach fruit ('Suncrest') grown at high (six leaves per fruit; Panels A - G) or low (18 leaves per fruit; Panels H - N) fruit load. The symbols and bars represent the means and ± standard deviations of the measurements (n = 5) and the lines are the predictions using the virtual fruit model.

agronomic standards. All three factors affected fruit quality without any strong interactions between them (Table I). Fruit DW at thinning had a large and positive effect on fruit size and on the percentage of flesh in the fruit at harvest. Similar results have been found in mango fruit (Léchaudel *et al*., 2005). Fruit size at thinning provides a good indicator of cell numbers in the fruit flesh, which is a major component of the potential for fruit growth (Westwood, 1967).

Fruit load always had a moderate or small effect on fruit quality attributes, as exemplified by the previous virtual experiment, probably because the C supply from

TABLE I
Components of variance in 'Zephir' peach fruit quality attributes (% of total variance) as a function of fruit dry weight at thinning [DW (t_0)*], fruit load, and plant water status* (Ψ)*,simulated using the virtual fruit model*

Factor	Fruit dry weight	Percentage of flesh in the fruit	Water content	Sweetness
DW (t_0)	76.8	79.1	20.4	11.9
Load	6.6	3.2	4.0	1.5
Ψ	9.1	13.8	69.8	79.7
DW (t_0) × Load	6.8	0.9	0.2	0.9
DW (t_0) × Ψ	0.5	1.8	0.0	0.1
Load × Ψ	0.2	1.2	5.4	5.6
Residuals	0.0	0.1	0.2	0.2

the tree compensated for the local C deficit, and because fruit DW at thinning had a dominant effect on the C-demand of fruit in ' Zéphir' peach. Stem water potential had a large and positive effect on fruit water content, and a negative effect on sweetness, which was expected through the process of dilution resulting from the supply of water.

In the final series of virtual experiments, a wide range of time schedules of water supply was simulated using 'Suncrest' peach fruit, starting from the observation that fruit crops often encounter alternate dry and humid periods, the duration of which can be highly variable because of unpredictable weather events, or various technical constraints. Within a framework of alternate dry and humid periods, this virtual experiment was aimed at answering the following questions: is there a relationship between time schedules of water supply and fruit quality at harvest? And, if so, which trait or traits in the time schedules was responsible for such a relationship? To address these questions, two series of 100-time schedules of water supply, each composed of six successive periods of alternating and contrasting water conditions, were set up. The periods were of random length, but the sum of the durations of the six periods in each time schedule was fixed by the duration of fruit growth. In the first series, the first period was dry (i.e., a water deficit represented by a mean stem water potential of -0.8 MPa). In the second series, the first period was irrigated by an irrigation system or by rainfall (i.e., normal water conditions as represented by a mean stem water potential of -0.5 MPa). The alternation of water conditions meant that each dry period was followed by a humid period, and *vice versa*.

Figure 4 shows these results of the experiments for two quality attributes: FW and fruit sweetness. The time-course of quality attributes fluctuated greatly, indicating the very reactive behaviour of the virtual fruit model. The analyses, undertaken separately for each of the two series described above, demonstrated that there was no relationship between the "global" pattern of time

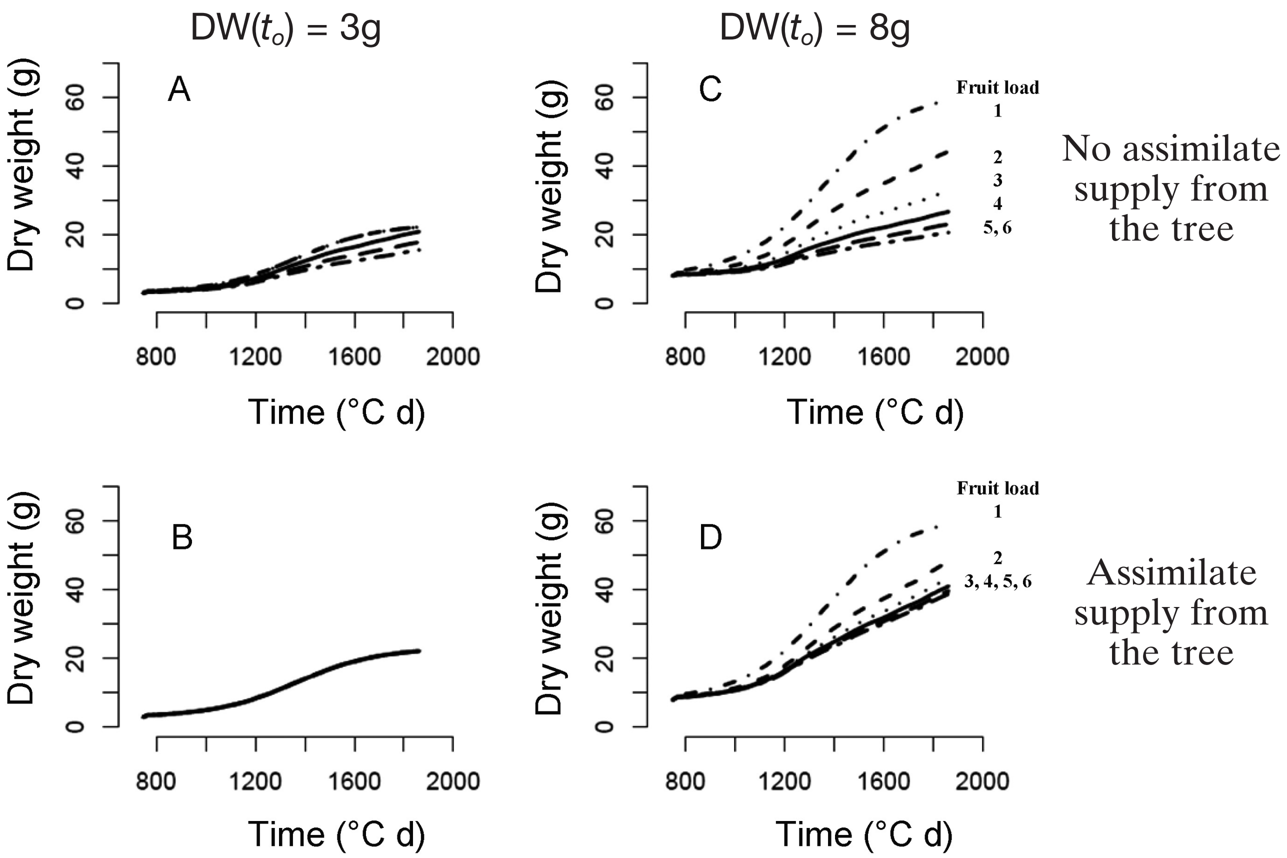

FIG. 3
Simulated effects of fruit dry weight [DW (t_0)] and fruit load at thinning (1 – 6 fruits per fruit-bearing shoot) on dry weight growth in peach fruit 'Zéphir' with no assimilate supply from the tree (Panels A, C), or with assimilate supply from the tree (Panels B, D).

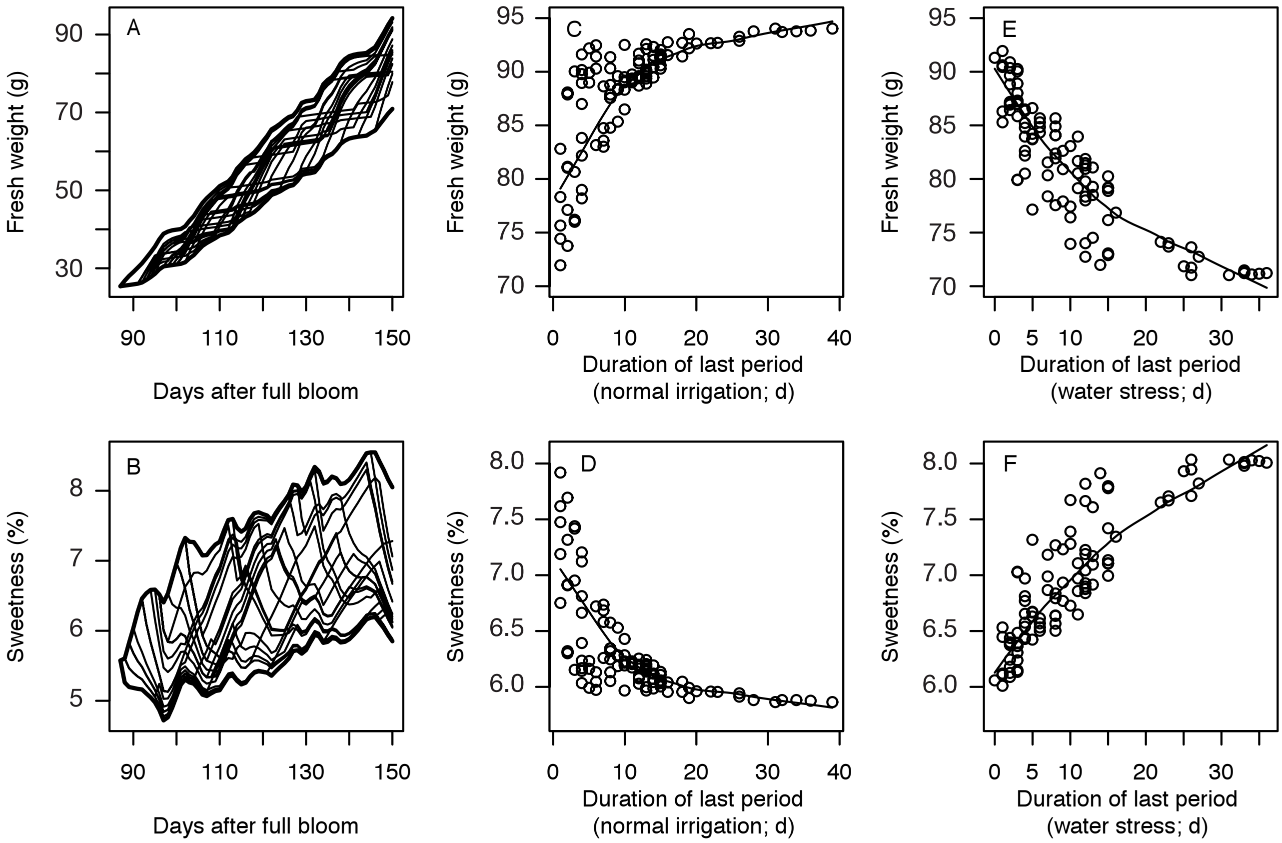

FIG. 4
Virtual experiment on the effects of various time schedules of water supply, with alternate periods of normal or water stress conditions of random length, on the fresh weight (FW) and sweetness of 'Suncrest' peach fruit. Panels A, B, time-course of quality attributes for 100-time schedules. The upper thick line in Panel A and the lower thick line in Panel B represent the case where the water supply was normal throughout fruit development. The lower thick line in Panel A and the upper thick line in Panel B represent the case where water supply was reduced throughout fruit development. Panels C – F, relationships between the duration of the last period of drought or water supply and the two quality attributes at harvest (smoothed curves). Panels C, D, time schedules that started with a dry period and ended with a humid period. Panels E, F, time schedules started with a humid period and ended with a dry period.

schedules of water supply and fruit quality at harvest (data not shown). The duration of each of the six periods, the total duration of the dry periods, and the total duration of the humid periods, were then tested as candidate variables. This exploratory analysis demonstrated that fruit quality at harvest could essentially be explained by the duration of the last period of the time schedule. The correlation was positive for FW and negative for sweetness in the case of time schedules that started with a dry period and ended with a humid period; and, conversely, negative for FW and positive for sweetness in the case of time schedules that started with a humid period and ended with a dry period.

These three virtual experiments clearly demonstrate that the virtual fruit model was "intelligent". It was able to reveal behaviours that would have been unpredictable when considering only the basic components of the model. It suggested that the main effect of alternate dry and humid periods was caused by the duration of the last period, which is of both theoretical and practical interest. It exemplifies the ability of the virtual fruit model to direct research into unknown abilities of the fruit system.

CONCLUSIONS AND PROSPECTS

In this study, we have shown the relevance of a multi-criterion, process-based model of fruit quality, a "virtual fruit model", by analysing environmental effects by means of virtual experiments. During these experiments, the virtual fruit model behaved like a true system, and showed emerging properties of both theoretical and practical interest. The model is therefore a useful contribution to SMARTFRUIT, within the ISAFRUIT Project, which aims to produce conceptual and methodological research tools to promote fruit consumption in Europe. It may also be especially helpful for applied research in agronomy and genetics.

The virtual fruit model provides a future opportunity for agronomy. It may help us to understand future experimental results not yet documented. Also, performing virtual experiments provides an opportunity to control factors that are difficult to control in the orchard, such as fruit size at thinning.

The virtual fruit model also provides an opportunity for genetics research. Geneticists still encounter two major difficulties. First, quality attributes that are breeding targets result from many overlapping processes and are thus controlled by many genes. Second, these characters are under the influence of the environment. This often results in strong genotype × environment interactions, which make genetic analyses, and their applications to breeding, difficult. Studying a quantitative attribute *via* the virtual fruit model made it possible to deal with both difficulties simultaneously. Instead of looking for QTLs that control an attribute directly, it is more efficient to look for QTLs that control the model parameters, because they are assumed to be independent of the environment. This approach was applied to peach fruit by Quilot *et al*. (2005a,b). Throughout studies on the co-location of QTLs for parameters and QTLs for attributes, the physiological meanings of QTLs for attributes have been proposed. This opens the way to design *in silico* ideotypes adapted to given requirements, which may constitute a basis for future breeding.

In addition, the virtual fruit model may provide an opportunity for ecology research. It may help to renewing studies on quantitative interactions between diseases or pests, and crops, by offering the possibility to go beyond classical yield losses (Gutierrez and Curry, 1989; Gutierrez *et al*., 1991; Rossing, 1991) and to take quality losses into account. It may also strengthen studies on qualitative interactions, by considering host susceptibility, that may affect the physical characteristics and chemical composition of fruit, including secondary metabolites that play a major role in defense (Tomás-Barberán and Espín, 2001; Cipollini *et al*., 2004; Dudareva and Negre, 2005).

In its present form, however, the virtual fruit model has some limitations. First, it is only for fruit. Nevertheless, fruit quality varies greatly, especially at the tree level (Audergon *et al*., 1993; Habib *et al*., 1991), under the influence of different horticultural practices. As research on virtual plants is expanding rapidly, we are currently incorporating the virtual fruit model into a virtual plant model that is able to react to horticultural operations (Génard *et al*., 2008). More generally, incorporating the virtual fruit model into a crop model will be valuable to simulate the combined effects of changes in climate, the development of pests that affect fruit directly or indirectly, genotype, and horticultural operations, on quality attributes. This should provide helpful information to improve crop breeding and crop management processes. Second, the virtual fruit model should be extended to include other fruit attributes. The current model considers Stage III of fruit growth, but features of cell division determine the fate of a fruit (Bertin *et al*., 2003). The range of quality attributes studied does not yet include secondary metabolites, such as natural defense components, or components that are advocated by national nutrition and health policies, and are key targets of the ISAFRUIT Project. Modelling, and virtual or real experiments, should progress simultaneously to overcome these limitations (Bertin *et al*., 2006). A modelling framework has been proposed to organise such research for a new generation of virtual fruit (Génard *et al*., 2007).

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