Modeling the effect of water supply on peach growth and sugar contents

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Abstract — Introduction. Water stress has been shown to affect the fruit quality, mainly by decreasing fruit weight and increasing sugar contents. In the future, irrigation scheduling will probably be based on simulations performed by models. Our aim was to create a model composed of two recently reported sub-models concerning peach fruit growth and fruit sugar content. **The model**. The model studied was restricted to the fruit. It first calculated fruit growth in fresh and dry matter according to the simple laws of water and carbon transfer into and out of the fruit (sub-model 1). Then, the flow of carbon calculated by sub-model 1 was used in sub-model 2 to simulate the temporal variation of sugar contents. The model inputs were temperature, global radiation and maximum daily trunk shrinkage (MDS). **Materials and methods**. Well-watered and water-stressed Dixired peach trees were used for calibrating and testing the model. **Simulations and discussion**. The model allowed to simulate the seasonal variation of fresh and dry weight, dry matter content of fruit and flesh sugars contents. The sucrose increased steadily especially during ripening whereas the other sugars were almost invariable. This behavior is typical of peach fruit accumulation of sugar. Similarly to our experimental data, the model did not predict any important variation of reducing sugars and sorbitol concentrations. The interaction between water stress and sap sugar concentration was investigated. **Conclusion**. We have shown that simple hypotheses on fluid flows made it possible to perform simulations of fruit growth and quality in reaction to water supply. The present model could be of help to manage daily irrigation according to the information obtained by the bio-indicator (MDS). (© Elsevier, Paris)

France / *Prunus persica* / peaches / simulation models / drought stress / dendrometry

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Modélisation de l'effet de l'irrigation sur la croissance et la teneur en sucres des pêches.

Résumé — Introduction. Le stress hydrique affecterait la qualité du fruit, principalement en diminuant son poids et en augmentant sa teneur en sucres. Dans l'avenir, l'irrigation devrait être programmée à partir des résultats de simulations données par des modèles. Notre objectif a été de créer un modèle constitué de deux sous-modèles récemment décrits, concernant la croissance de la pêche et sa teneur en sucres. **Le modèle**. Le modèle étudié se rapporte au seul fruit. D'abord, il calcule la croissance de ce fruit en matières fraîche et sèche à partir de simples lois de transfert du carbone et de l'eau à l'intérieur et hors du fruit (sous-modèle 1). Ensuite, le flux de carbone calculé par le sous-modèle 1 est utilisé dans le sous-modèle 2 pour simuler la variation dans le temps de la teneur en sucres. Les entrées du modèle sont la température, la radiation globale et le maximum de contraction diurne du tronc (MCDT). **Matériel et méthodes**. Des pêchers de la variété Dixired, soit bien irrigués, soit soumis à un stress hydrique, ont été utilisés pour calibrer et tester le modèle. **Simulations et discussion**. Le modèle a permis de simuler les variations saisonnières de poids frais et sec et celles des teneurs en matière sèche et en sucres dans la chair. Le saccharose a augmenté progressivement, surtout pendant la maturation, alors que les autres sucres n'ont presque pas varié. Ce comportement est typique de l'accumulation de sucres dans la pêche. De même que nos données expérimentales, le modèle n'a pas montré d'importantes variations des teneurs en sucres réducteurs et en sorbitol. L'interaction entre le stress hydrique et le taux de sucres dans la sève a été étudiée. **Conclusion**. De simples hypothèses de circulation des fluides ont donc permis d'effectuer des simulations de la croissance du fruit et de sa qualité en réponse à un stress hydrique. Le modèle présenté pourrait aider à gérer l'irrigation au jour le jour à partir des informations données par le bio-indicateur (MCDT). (© Elsevier, Paris)

France / *Prunus persica* / pêche (fruits) / modèle de simulation / stress dû à la sécheresse / dendrométrie

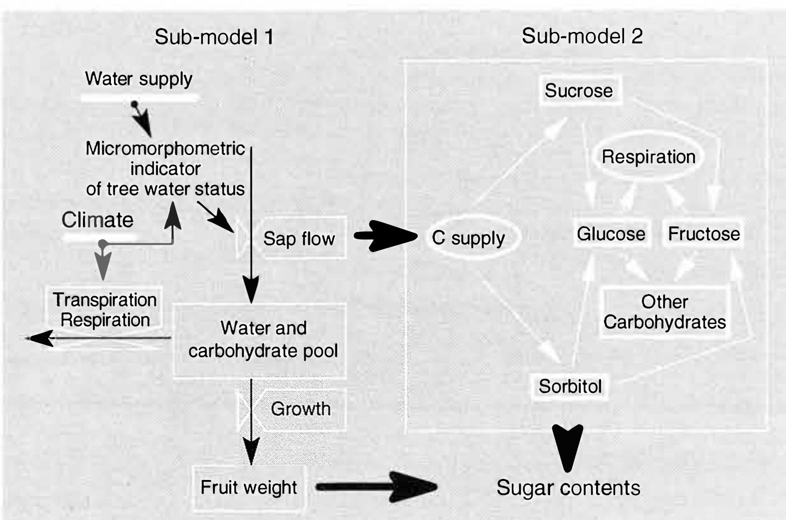
1. introduction

Fruit trees, mostly cultivated in dry countries, are often subjected to water stress. This stress has been shown to affect the fruit quality, mainly by decreasing fruit weight and increasing sugar contents [1, 2]. In order to schedule irrigation, growers have to be able to predict the effect of water deficit on fruit quality. In the future, this irrigation scheduling will probably be based on simulations performed by models, as shown in Buwalda and Atkins [3] for a variety of horticultural practices. Our aim was to create a model composed of two recently reported sub-models concerning peach fruit growth [4] and fruit sugar content [5], respectively. We describe how to use this model for analysing the effect of water stress on fruit quality. We conclude by considering some perspectives on fruit modeling.

2. the model

The model in *figure 1* was restricted to the fruit. It assumed that trees were optimally fertilized and carbon acquisition by photosynthesis was sufficient for well-irrigated trees to reach their full fruit growth potential.

Figure 1.
Diagram illustration of two sub-models and corresponding links. In the first sub-model, rectangles represent state variables, valve symbols represent flows of water and carbon and external variables are underlined. The arrows with no valve symbol represent flows of information.
In the second sub-model, the arrows, ellipses and rectangles represent carbon flows, carbon supply and losses, and carbohydrate components, respectively. The coefficient associated to each flow is indicated by F_i (i =1 to 4, see text).



The model first calculated fruit growth in fresh and dry matter according to the simple laws of water and carbon transfer into and out of the fruit (sub-model 1). Then, the flow of carbon calculated by sub-model 1 was used in sub-model 2 to simulate the temporal variation of sugar contents. The model inputs were temperature, global radiation and maximum daily trunk shrinkage (MDS). We chose MDS as an indicator of plant water status because it varied according to the water content of peach trees [6] and was thus functionally related to tree water potential [7]. Moreover, MDS was successfully used for irrigation scheduling [8].

2.1. sub-model 1

This sub-model has been thoroughly described and discussed in Génard and Huguet [4]. The fruit received a daily solution flow from the plant (F) and lost water by transpiration (T) and carbon by respiration.

The maintenance respiration was a function of dry mass and was a Q10 function of temperature. Growth respiration was a function of absolute growth rate expressed in dry matter. Daily transpiration, calculated as the sum of hourly transpiration, was a function of fruit weight (W), hourly global solar radiation (GR) and skin area of the fruit (A):

$$T = A \cdot \sum T_{hmax} \cdot (1 - e^{\beta \cdot W \cdot GR})$$

where T_{hmax} was the maximum hourly transpiration per unit area of skin, β a parameter and A was calculated from an empirical relation of fruit weight.

The sap flow (F) was calculated as an increasing function of fruit transpiration because we assumed that the osmotic potential of the fruit decreased as transpiration increased. The effect of water supply on sap flow was considered through MDS in the function:

$$F = A_1 \cdot (1 - e^{-A_2 \cdot T^{A_3}})$$

with $$A_i = a_i \cdot \left(\frac{MDS}{MDS_0}\right)^{b_i} \; if \; F < F_{max}$$

where a_i, b_i, MDS_0 and F_{max} were parameters.

The sap flow increased according to calculated transpiration rate and leveled off at lower values when MDS/MDS_0 increased, i.e., when water stress was greater.

We added an equation to the model presented by Génard and Huguet [4] to calculate the phloemic flow (F_{ph}). This flow was modeled as a function of fruit fresh weight, which was consistent with our experimental results (data not shown):

$$F_{ph} = c1 \ W^{c2}$$

Assuming a constant dry matter concentration (d) in the phloem sap, the flow of carbon into the fruit was calculated as:

$$\frac{dC_{ph}}{dt} = F_{ph} \cdot d \cdot cfl$$

where cfl was the carbon content of dry matter.

This flow of carbon into the fruit was the main input in the sub-model 2 .

2.2. sub-model 2

The main components of this sub-model were described and discussed in Génard et Souty [5]. It simulated the partitioning of carbon coming from the phloem into sorbitol, sucrose, glucose, fructose, and other carbohydrates in the fruit as well as CO_2 produced through the respiration process. The link between each compartment was the carbon flow. Each flow exiting a compartment i (except respiration) was the product of the carbon content in i by a coefficient F_{ix}, which was either a constant or a function of degree-days (dd). The temporal variation of the carbon amount in a compartment × was the balance between the carbon flow entering and exiting this compartment:

$$\frac{dC_x}{dt} = E_x + \sum_{i \neq x} F_{ix}(k_{ix}, dd) \cdot C_i - \sum_{j \neq x} F_{xj}(k_{xj}, dd) \cdot C_x - R_x$$

where Ex and Rx, which can be null, were the carbon flow from the phoemic sap and the carbon outflow to the respiration, respectively.

The sugar concentration for a sugar "x" (SCx) was computed as:

$$SC_x = \frac{100 C_x}{c_x FW}$$

where c_x was the carbon content in 1 g of this sugar and FW is the flesh fresh weight.

3. materials and methods

Our data were taken from an experiment that compared well-watered and water-stressed Dixired peach trees. The level of water stress for each treatment is illustrated in *figure 2* by the temporal variation of the MDS of the trunk. This experiment, which is described by Huguet and Génard [2], was conducted at Montfavet Inra centre in southern France and was used for calibrating and testing the model. The model runs on a daily basis. Differential equations were solved numerically using the first-order Runge Kutta method [9]. Most parameters used for the simulations were taken from Génard and Huguet [4] for sub-model 1, and an experiment in Génard and Souty [5] for the sub-model 2. The parameters $c1$ and $c2$ of the equation used to calculate phloemic flow were estimated by fitting the model to the data from other experiments on Suncrest and Bigtop cultivars, presented in Huguet et al. [10]. A nonlinear fit was carried out using the least-squares method.

The dry matter concentration of phloem sap (parameter d) was estimated. As ki parameters for submodel 2 had previously been estimated for the Suncrest cultivar, they were partly used for the Dixired cultivar. The values of two ki parameters only were re-estimated to better fit the Dixired data. These estimations were calculated by minimizing the difference between simulated and observed data from the well-watered treatment. The variables considered for the fit were dry and fresh weight at harvest for d, and sugar concentrations at harvest for ki. The model was tested using Dixired data from the water-stressed treatment.

4. simulations and discussion

Parameters $c1$ and $c2$ were estimated as 0.0028 and 1.535, respectively. The phloemic concentration d was estimated as 0.28 $g \cdot cm^{-3}$, which is a possible value for phloem sap

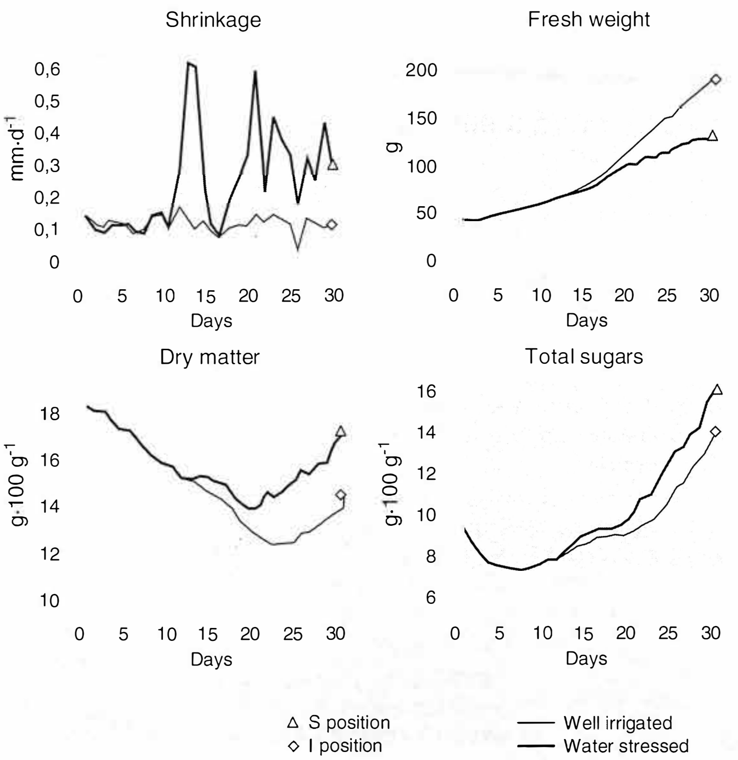


Figure 2.
Maximum daily shrinkage of trunk (observed data), and simulations of the variation of fruit fresh weight, flesh dry matter content and total sugar content for well-irrigated (thin curve) and water-stressed (thick curve) trees.
The positions of I and S on each graph indicates the observed values at harvest in well-irrigated and water-stressed trees, respectively.

[11] and is close to the measurements of Escobar-Gutiérrez [12] in peach seedlings. Changes in two *ki* values, in comparison with original values estimated for Suncrest cultivar [5], indicated that the amount of sucrose was higher in the phloem sap of Dixired, and reducing sugars were used more actively for cell synthesis in Dixired than in Suncrest.

For well-watered trees used for model calibration, there was a close agreement between measured fresh fruit weight at harvest and model outputs (*figure 2*). Similar agreements were obtained for dry matter and sugar content (*figures 2, 3*). The model simulated fairly well the hierarchy between sugar concentrations: sucrose > glucose or fructose > sorbitol, as observed by fruit analyses [13, 14].

The model allowed to simulate the seasonal variation of fresh and dry weight, dry matter content of fruit and flesh sugars contents. The sucrose increased steadily especially during ripening whereas the other sugars were almost invariable. This behavior is typical of peach fruit accumulation of sugar as shown by Ishida et al. [13] and Chapman et al. [15]. The test on water-stressed trees was conclusive (*figures 2, 3*). The model simulated the observed decrease of fruit weight and the increase of sucrose content. Similarly to our experimental data, it did not predict any important variation of reducing sugars and sorbitol concentrations.

The interaction between water stress and sap sugar concentration was investigated. When we applied a stress to a tree, we could consider two cases: either the stress can simply limit the water availability or the stress can also limit the sugar availability by depressing the photosynthesis and inducing a decrease of the phloemic sap sugar concentration [16]. These two situations were simulated considering that stress acts or not on the phloemic sap sugar concentration (*figure 4*). In the first case, the model simulated an increase of the dry matter content in comparison with the well-irrigated tree. This situation seems to be the most frequently observed and was noted for Dixired peach cultivar. To simulate the second case, we considered that the phloemic sap sugar concentration had decreased from 0.3 $g \cdot g^{-1}$ to 0.1 $g \cdot g^{-1}$ with the application of the stress. This resulted in a lower dry matter content at harvest than for the well-irrigated tree. We observed such a situation for the cultivar Bigtop.

5. conclusion

We have shown that simple hypotheses on fluid flows made it possible to perform simulations of fruit growth and quality in reaction to water supply. The present model could be of help to manage daily irrigation (tactical decision) according to the information obtained by the bio-indicator. However, we saw that the interaction between carbon supply and water stress is also relevant. Ben Mimoun et al. [17] suggested creating a carbon-based model that would focus on this aspect. Connecting the two approaches seems a promising idea.

In the future, we believe that it will be possible to connect this fruit model to a tree using an integrative approach on tree functioning [18]. The effect of different water management strategies on the whole plant will be simulated according to hypotheses on climate and soil. This will enable growers to test new horticultural techniques and create new areas suitable for fruit production.

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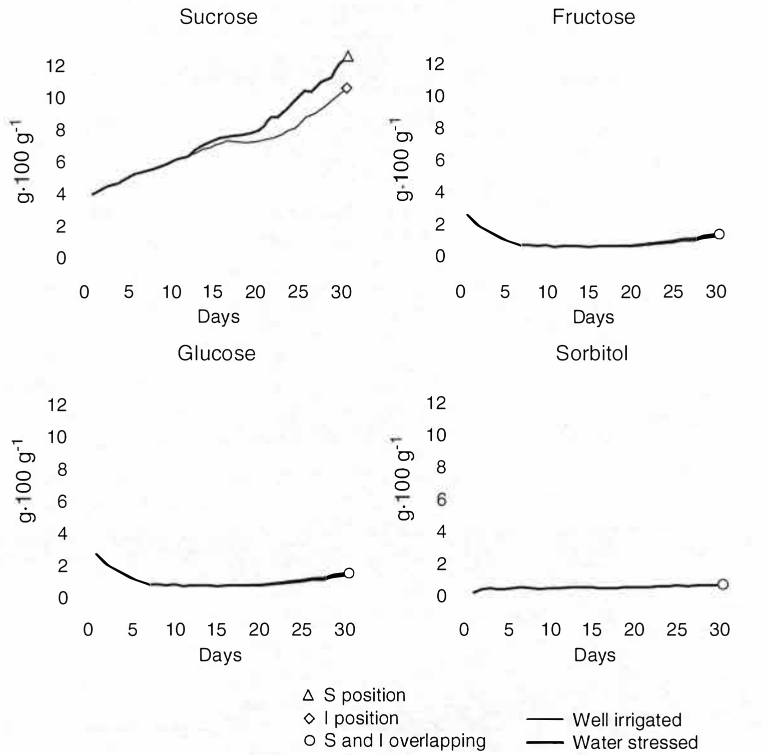

Figure 3.
Simulations of sucrose, glucose, fructose and sorbitol contents in fruit flesh of well-irrigated (thin curve) and water-stressed (thick curve) trees. The positions of I and S on each graph indicates the observed values at harvest in well-irrigated and water-stressed trees, respectively.

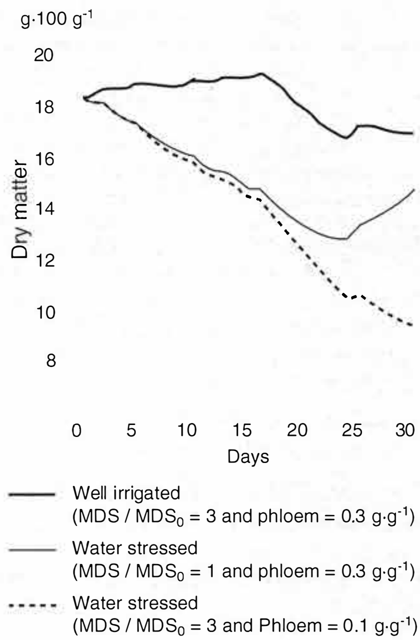

Figure 4.
Simulations of flesh dry matter content in fruits of well-irrigated or water-stressed trees, according to phloem sap sugar concentration. Well-irrigated trees shrink less ($MDS/MDS_0 = 1$) than those in stressed conditions ($MDS/MDS_0 = 3$) (MDS = maximum daily trunk shrinkage). Two types of simulations were performed in stressed conditions: with or without the stress effect on phloem sugar concentration, which either remains equal to 0.3 $g \cdot g^{-1}$ or decreases to 0.1 $g \cdot g^{-1}$.

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Modelización del efecto del riego en el crecimiento y el contenido de azúcares de los melocotones.

Resumen — Introducción. El estrés hídrico afectaría la calidad de la fruta, principalmente al disminuir su peso y al aumentar su contenido de azúcares. En lo sucesivo, el riego debería programarse a partir de los resultados de simulaciones dadas por modelos. Nuestro objetivo fue crear un modelo constituido de dos submodelos recientemente descritos, concerniendo el crecimiento del melocotón y su contenido de azúcares. **El modelo**. El modelo estudiado se refiere sólo a la fruta. En primer lugar, calcula el crecimiento de esta fruta en materias fresca y seca a partir de sencillas leyes de transferencia del carbono y del agua dentro y fuera de la fruta (submodelo 1). Más tarde, el flujo de carbono calculado por el submodelo 1 se utiliza en el submodelo 2 para simular la variación en el tiempo del contenido de azúcares. Las entradas del modelo son la temperatura, la radiación global y el máximo de contracción diurna del tronco (MCDT). **Material y métodos**. Se utilizaron melocotoneros de la variedad Dixired, ya sea bien irrigados, ya sea sometidos a un estrés hídrico, para calibrar y someter a prueba el modelo. **Simulaciones y discusión**. El modelo permitió simular las variaciones temporales de peso fresco y seco y las de los contenidos en materia seca y en azúcares en la carne. La sacarosa aumentó progresivamente, sobre todo durante la maturación, mientras que los demás azúcares casi no variaron. Este comportamiento es típico de la acumulación de azúcares en el melocotón. Lo mismo que nuestros datos experimentales, el modelo no mostró importantes variaciones de los contenidos de azúcares reductores y de sorbitol. Se estudió la interacción entre el estrés hídrico y la tasa de azúcares en la savia. **Conclusión**. Meras hipótesis de circulación de los fluidos permitieron pues realizar simulaciones del crecimiento de la fruta y de su calidad como respuesta a un estrés hídrico. El modelo presentado podría ayudar a manejar el riego día a día a partir de las informaciones dadas por el bio-indicador (MCDT).

Francia / *Prunus persica* / durazno / modelos de simulación / estrés de sequía / dendrometría