

Modeling carbon allocation in peach shoot bearing fruits: simulation of the water stress effect

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Modeling carbon allocation in peach shoot bearing fruits: simulation of the water stress effect.

Abstract — Introduction. An existing model describing the source-sink relations of girdled peach stems was modified to account for the effect of water stress on growth. **The model.** The model predicts fruit growth and reserve status based on sink demand, leaf number and environmental effects, including that of the leaf water potential. A decrease in fruit dry weight is predicted with increasing water stress. **Simulations.** The effects of low water potential on fruit dry weight depend upon the leaf/fruit ratio. At high leaf/fruit ratios, water stress has less influence on fruit growth. At low leaf/fruit ratios, water stress severely limits fruit size. Reserves act as a buffer against the effects of water stress. Simulations showed that the timing of water stress affects fruit dry weight and the level of reserves. **Discussion and conclusion.** the model with its different outputs can represent an interesting tool to understand the interactions between source and sink factors. This is a necessary step to explain and reduce fruit growth variability. The simulations with regards to water stress must be validated by experiments. (© Elsevier, Paris)

France / *Prunus persica* / growth period / drought stress / simulation models / source sink relations

Modélisation de la répartition du carbone dans des rameaux mixtes de pêchers : simulation de l'effet d'un stress hydrique.

Résumé — Introduction. Un modèle existant, décrivant les relations sources-puits dans des rameaux mixtes de pêcher isolés du reste de l'arbre, a été modifié pour prendre en compte l'effet du stress hydrique sur la croissance des fruits. **Le modèle.** Le modèle décrit la croissance des fruits et l'état des réserves en se basant sur la demande des puits, le nombre de feuilles et les effets de l'environnement, y compris le potentiel hydrique foliaire. Il prédit que le poids sec du fruit diminue en même temps qu'augmente le stress hydrique. **Simulations.** Les effets d'un faible potentiel hydrique sur le poids sec des fruits dépendent du rapport feuille/fruit. Lorsque ce rapport est élevé, le stress hydrique a moins d'influence sur la croissance des fruits. Lorsque le rapport feuille/fruit est faible, le stress hydrique limite sévèrement la croissance des fruits. Les réserves tamponnent les effets du stress hydrique. Les simulations ont montré que le moment où intervient le stress hydrique a une influence sur le poids sec du fruit et le niveau des réserves. **Discussion et conclusion.** Le modèle et les différentes informations qu'il fournit peut s'avérer un outil intéressant pour comprendre les interactions entre les facteurs sources et puits. Cela constitue une étape nécessaire pour expliquer et réduire la variabilité de la croissance des fruits. Les simulations concernant le stress hydrique devront être validées par des expérimentations. (© Elsevier, Paris)

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1. introduction

The variability of peach growth within the tree is high and its management is a challenge for fruit growers because fruit size is an important criterion for determining orchard profitability. A theoretical frame using the source-sink concept is a way to understand and explain this variability. Moreover, a modelling approach is interesting to synthesise knowledge concerning the assimilate production by the sources, their partitioning between the different sinks, and the characteristics of fruit growth. A model of carbon assimilation and allocation in an isolated shoot-bearing fruit was developed to meet these aims [1] and tested in the case of peach [2]. However, this model does not account for water stress effects.

Peach trees are frequently cultivated in dry countries and are often subject to water stress which influences fruit growth. Berman and DeJong [3] reported that fruit growth is differentially sensitive to water stress at different times of the season.

So, the objective of this work is to present a modification of the model, which makes it possible to simulate the fruit growth variability observed in peach trees under different water status. The paper will present some simulations dealing with the level and timing of water stress for the sake of illustration.

2. the model

The previous version of the model has been extensively described in [1]. It is summarised below.

The system represented by the model is a shoot bearing fruits defined as three compartments: fruits, stem, and leafy shoots comprising the leaves and the growing shoots themselves. The leafy shoot and the stem compartments comprise a structure part and a reserve part. "n" identical organs compose the fruit and leafy shoot compartments. Thus, the variability described by the model is that observed among the different shoots bearing fruits of the tree.

The model is composed of three modules concerning the carbon production, the carbon allocation and the kinetic of the carbon reserves.

The daily assimilate production is computed as the integral of the hourly photosynthesis, by using the values of the incident radiation issued from hourly climatic databases. The calculation separates the total leaf area into a sunlit and a shaded component, using hourly fractions of sunlit leaves taken from databases describing shoot light environments. The hourly photosynthesis depends on the maximal light saturated photosynthesis, which is regulated by the leaf assimilate status: the accumulation of assimilates in the leaf decreases the light saturated photosynthesis. Carbon assimilation by fruits is also considered.

The carbon provided by photosynthesis is first used to fulfil the maintenance respiration of the different components of the system. The remaining carbon is allocated to shoot growth and then to fruit growth. The carbon allocation to a given sink depends on its demand. The sink demands are based on analytical formulations of the potential growth at any time in terms of degree days and accumulated growth.

The reserves play a buffer role between the acquisition of carbon and its use by the different sinks. If the assimilates provided by the photosynthesis are not sufficient for the different demands, an amount of the assimilates is mobilised from the reserve part. This amount is a constant proportion of the total quantity of the reserves in the stem and in the shoot, but the reserves of the shoot are mobilised more easily than the reserves of the stem. When there is a carbon remainder from current photosynthesis after the supply of the different sinks, it is allocated to the shoot reserves and then to the stem reserves as soon as the shoot reserve compartment is saturated.

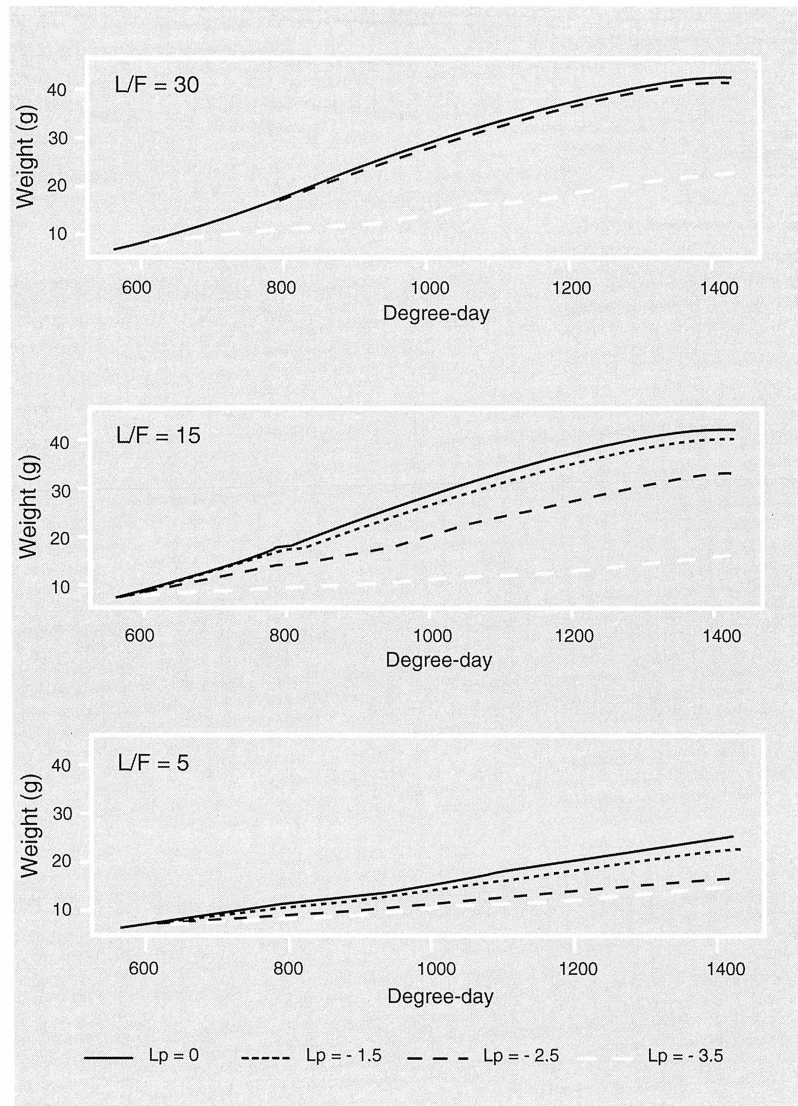
This version of the model has been parameterized for peach, with consideration of two cultivars and locations [1]. It has been tested in different situations and indicated good performance, especially concerning the variability of fruit growth responding to the variation of source and sink factors [2].

The following modification of the model concerns the formulation of the maximal photosynthesis. We assume that under a water stress, the maximal photosynthesis decreases through a reduction of the stomatal conductance, which agrees with different works [4–6]. This assumption was analysed through an empirical relationship between maximal photosynthesis (P_{\max} in $\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and leaf water potential (Ψ_{leaf} in MPa), which gives an indication of the water stress degree. This relationship was fitted to the data of [7]: $P_{\max} = P_{\max}[0] \cdot (1 - \exp[4.43 (1/\Psi_{\text{leaf}} + 0.22)])$, with $P_{\max}[0]$ the maximal photosynthesis without water stress.

This point of view deals directly with source limitation. However, sink limitation is also considered because of the formulation of sink demands in the model (see above). When the tree has started to experience water stress, the photosynthesis is affected so that carbon allocation and thus growth are reduced. The following sink demands are able to attest this effect since they depend on the accumulated growth at any time.

3. simulations

The model was used to simulate the effect of either the level or the time of application of water stress during fruit growth for different leaf/fruit ratios (L/F): 30, 15 and 5. The conditions were inspired by an experiment previously used to test the model [2] that had been performed in Gotheron (Inra experimental station) during year 1994. The meteorological data were drawn from the Inra climatic database. The simulated system was a shoot in a good light environment, with six leafy shoots having each 5 leaves and either 1, 2 or 6 fruits according to the leaf/fruit ratio. The simulation started at 560 degree days (dd) after bloom and was completed at 1 435 dd after bloom. At the beginning of the simulation, the mean dry weights were 20 g, 2.2 g and 6.6 g per stem, leafy shoot and fruit, respectively.



3.1. water leaf potential level

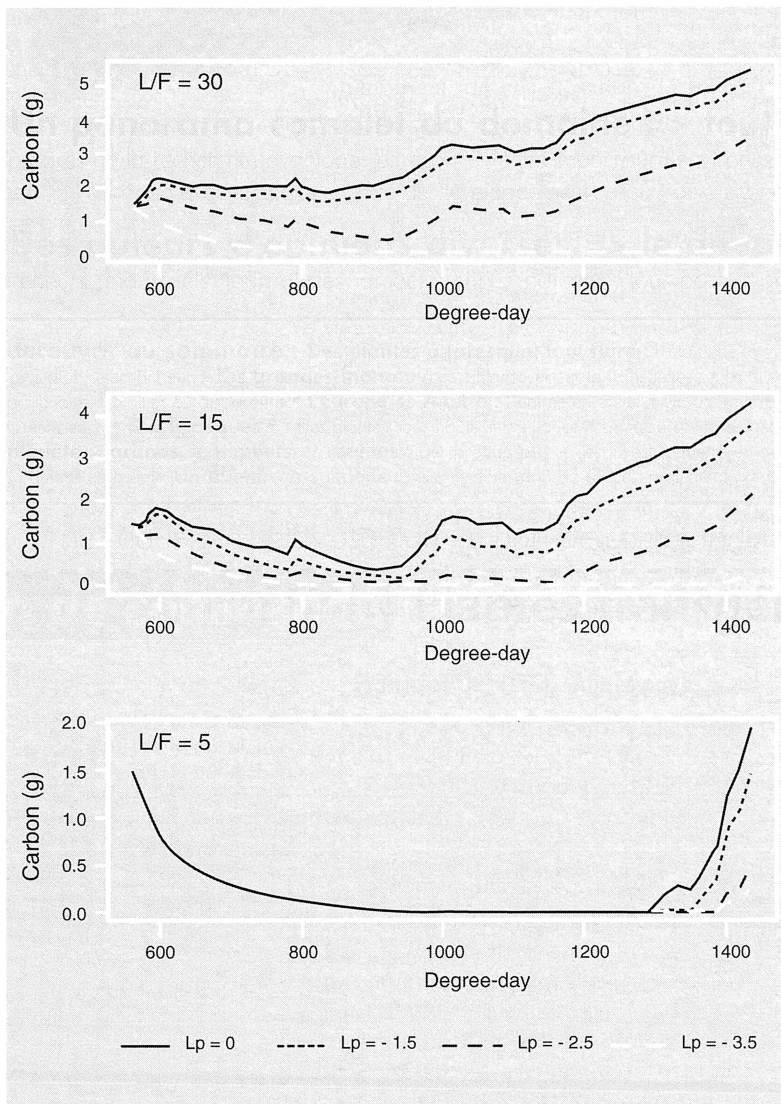
The model was run using different Ψ_{leaf} values varying from 0 to -3.5 MPa.

According to the model, fruit growth is affected by water stress, but this effect depends on L/F (figure 1). For the highest L/F, water stress reduces fruit growth only for $\Psi_{\text{leaf}} = -3.5$ MPa. For the median and low L/F, the decrease in fruit growth begins with $\Psi_{\text{leaf}} = -1.5$ MPa. The reduction in fruit growth can represent 50% of the fruit growth under well-watered conditions.

Figure 1. Simulation of the effect of different leaf water potentials (L_p , expressed in MPa) on fruit growth according to degree days after full bloom, for different leaf/fruit ratios.

For a given L/F, the reserve kinetic is affected by Ψ_{leaf} variation (figure 2). For L/F = 30 or 15, the level of the reserves is reduced by the decrease in Ψ_{leaf} and it reaches zero for $\Psi_{\text{leaf}} = -3.5$ MPa. For L/F=15, the level of the reserves decreases at the beginning of the simulation and then increases. For L/F = 5, the reserves decrease during the simulation to a nil value for all the Ψ_{leaf} values, and recover their level at the end of the simulation.

Figure 2. Simulation of the effect of different leaf water potentials on the kinetic, according to degree days after full bloom, of carbon reserves (of leafy shoots and stem considered together) for different leaf/fruit ratios.



3.2. time of application of water stress

In these simulations, a Ψ_{leaf} of -2.5 MPa was applied either between 560 and 1 000 dd after full bloom or from 1 000 dd to fruit maturity.

According to the model, fruit growth is affected by water stress when the L/F is 15 or 5 (figure 3).

Fruit growth is more penalised when water stress occurs at the beginning of the third phase of fruit growth (main period of flesh growth), than when it occurs at the end of growth in the case of L/F = 15. For 5 leaves per fruit, fruit growth reaches the same dry weight at the end of the simulation in both cases, but fruit weight is so small that it is not interesting for commercialisation.

For L/F = 30 and 15, the reserves decrease during the water stress, as compared to the well-irrigated case (figure 4). When the stress is applied early, at the end of the simulation the reserve level is equal to that obtained in the non-limiting case. For L/F = 5, the reserves decrease during the simulation to the nil level whatever the time of water stress application.

4. discussion and conclusion

After the model, the variation of Ψ_{leaf} induced by a water stress affects the production and the partitioning of assimilates. This effect of Ψ_{leaf} depends on the L/F ratio, and more generally on the source conditions. This result can be explained by the difference of the assimilate production between L/F treatments and the role of reserves as a buffer. For L/F = 30, the reduction of the assimilate supply due to the water stress was counterbalanced by the reserves except when the value of Ψ_{leaf} was -3.5 MPa. In the latter case, all the reserves were mobilised and fruit growth was affected, which indicated that for an important crop load, the reserve mobilisation cannot eliminate the effect of water stress. This result agrees with those obtained by Berman and DeJong [3] who observed an

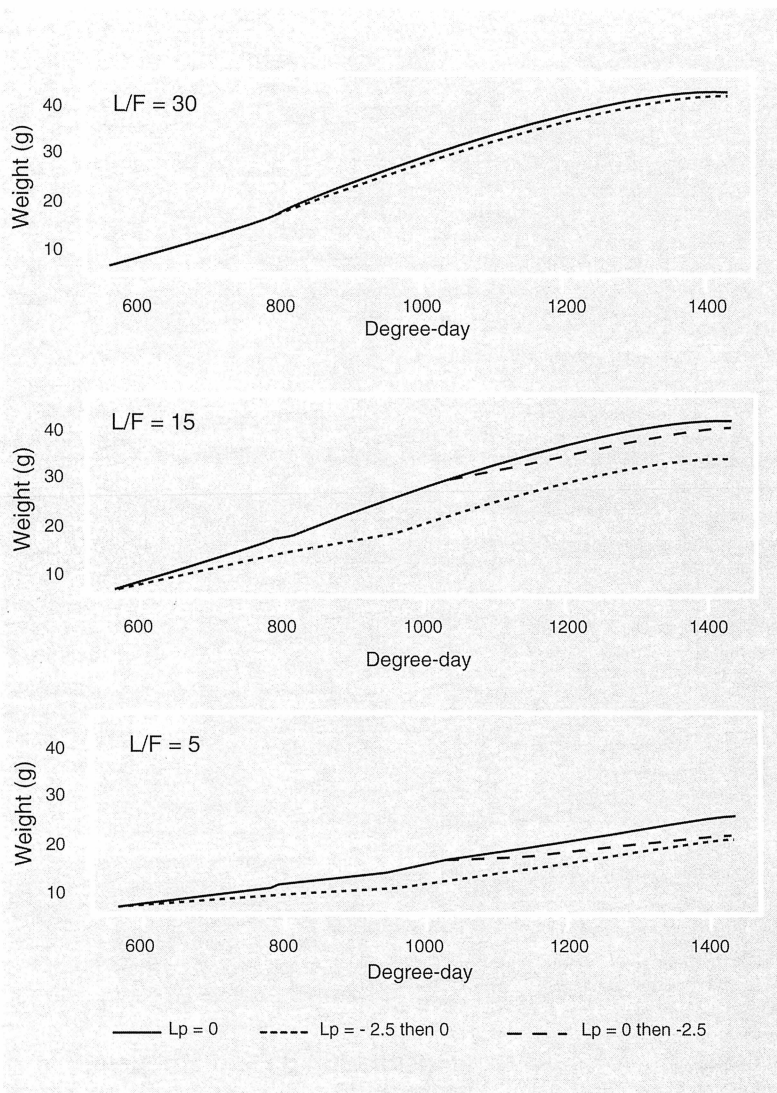
increase in the degree of water stress effect with increasing crop load. In their experiments, the water stress did not reduce the fruit dry weight for light and moderate crop loads but only for a high one.

The time of the occurrence of the water stress for a given L/F ratio is also important. According to the model, fruit growth is more penalised when the stress occurs during the beginning of the third fruit growth stage. This period corresponds to a very rapid fruit growth and to a high fruit demand, so that it could be very sensitive to a decrease in the assimilate availability [8]. Our result agrees with the conclusions of Li et al. [9] who stated that the final period of fruit growth is more sensitive to the water stress in peach, and with those of Mitchell and Chalmers [10] who did not see any water stress effect on fruit growth when it was applied during the slow fruit growth.

In conclusion, the model with its different outputs can represent an interesting tool to understand the interactions between source and sink factors. This is a necessary step to explain and reduce fruit growth variability. The simulations with regards to water stress must be validated by experiments. When validated in this way, the model might be used to test the effect of different times or levels of water stress applications for a peach shoot bearing fruits for different varieties and localities. Also, the present model could be easily connected to another model simulating the fruit sugar contents in relation to fruit growth [11]. A first attempt was made [12] but it concerns only well-irrigated conditions. This connection could be interesting to study the effect of water stress on fruit quality and not only on fruit dry weight.

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Figure 3.

Simulation of the effect of two times of application of water stress on fruit growth according to degree days (dd) after full bloom, for different leaf/fruit ratios. The change in the leaf water potential (L_p , expressed in Mpa) occurs at 1 000 dd after full bloom.

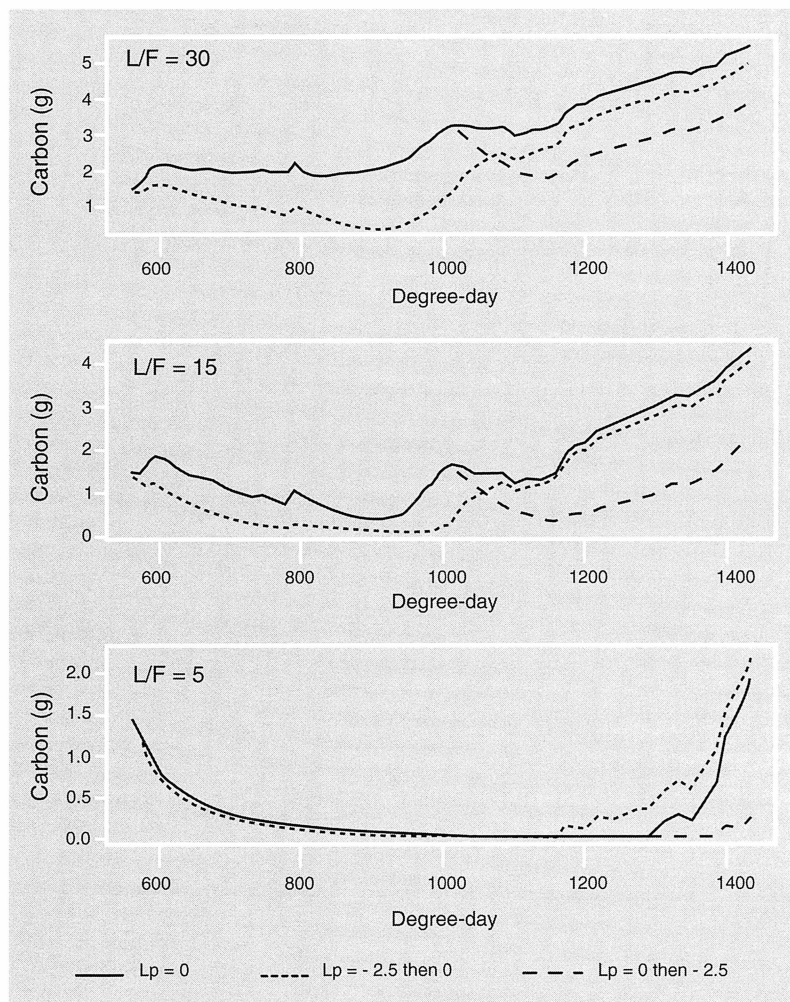


Figure 4. Simulation of the effect of two times of application of water stress on the kinetic, according to degree days (dd) after full bloom, of carbon reserves (of leafy shoots and stem considered together) for different leaf fruit ratios. The change in the leaf water potential (L_p , expressed in Mpa) occurs at 1 000 dd after full bloom.

Modelización de la distribución del carbono en ramos de melocotoneros llevando frutas: simulación del efecto de un estrés hídrico.

Resumen — Introducción. Se modificó un modelo existente describiendo las relaciones fuente-pozo en el tallo del melocotonero para tomar en cuenta el efecto del estrés hídrico en el crecimiento del árbol. **El modelo.** El modelo prevé el crecimiento de la fruta y el estado de las reservas basándose en el requerimiento del pozo, el número de hojas y los efectos del medio ambiente, incluido el potencial hídrico de la hoja. Predice que el peso seco de la fruta disminuye a la misma vez que aumenta el estrés hídrico. Los efectos de un bajo potencial hídrico sobre el peso seco de la fruta dependen de la relación hoja/fruta. Cuando esta relación es elevada, el estrés hídrico tiene menos influencia en el crecimiento de fruta. Cuando este valor hoja/fruta es bajo, el estrés hídrico limita severamente la dimensión de la fruta. Las reservas tamponan los efectos del estrés hídrico. **Simulaciones.** Las simulaciones mostraron que el momento en que interviene el estrés hídrico tiene una influencia sobre el peso seco de la fruta y el nivel de las reservas. **Discusión y conclusión.** El modelo y las distintas informaciones que proporciona puede revelarse una herramienta interesante para comprender las interacciones entre los factores fuente y pozo. Esto constituye una etapa necesaria para explicar y reducir la variabilidad del crecimiento de la fruta. Las simulaciones concerniendo el estrés hídrico tendrán que validarse mediante experimentaciones. (© Elsevier, Paris)

Francia / *Prunus persica* / periodo de crecimiento / estrés de sequía / modelos de simulación / relaciones fuente sumidero

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