Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree

José Manuel Miras Avalos, Rosalía Alcobendas, Juan José Alarcón, Pierre Valsesia, Michel M. Génard, Emilio Nicolás

▶ To cite this version:

José Manuel Miras Avalos, Rosalía Alcobendas, Juan José Alarcón, Pierre Valsesia, Michel M. Génard, et al.. Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 2013, 128, pp.1-12. 10.1016/agwat.2013.06.008 . hal-02643177

HAL Id: hal-02643177
https://hal.inrae.fr/hal-02643177

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

AGRICULTURAL WATER MANAGEMENT

Type of paper: Original paper (Regular paper)

Title: Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree

Authors names and addresses:

José M. **Mirás-Avalos**[1,2], Rosalía **Alcobendas**[3,4], Juan José **Alarcón**[3,4], Pierre **Valsesia**[5], Michel **Génard**[5], Emilio **Nicolás**[3,4]

[1] Facultad de Ciencias. Universidade da Coruña. Campus de A Zapateira s/n. A Coruña, Spain.
[2] Present address: Estación de Viticultura y Enología de Galicia (EVEGA). Ponte San Clodio s/n 32427, Leiro (Ourense), Spain
[3] Departamento de Riego, Centro de Edafología y Biología Aplicada del Segura, CSIC, P.O. Box 164, 30100, Espinardo (Murcia), Spain
[4] Unidad Asociada al CSIC de Horticultura Sostenible en Zonas Áridas (UPCT-CEBAS), Paseo Alfonso XIII, s/n. 30203, Cartagena (Murcia), Spain
[5] UR1115 Plantes et Systèmes de Culture Horticoles (PSH), INRA, Domaine Saint-Paul, Site Agroparc, 84914 Avignon Cedex 9, France

Corresponding author: José Manuel **Mirás-Avalos**
Estación de Viticultura y Enología de Galicia (EVEGA). Ponte San Clodio s/n 32427, Leiro (Ourense), Spain
Phone: +34 988 488033
Fax: +34 988 488191
E-mail: jmirasa@udc.es

Number of tables: 5
Number of figures: 6
Page count: 37 (including this one)

Research highlights:

- A middle-late maturing peach cultivar was successfully implemented into QualiTree.
- QualiTree was able to adequately simulate the effects of water stress on fruit growth.
- Fructose, glucose and sorbitol contents in the fruit flesh were well simulated.
- Water stress increased sugar contents in the fruit flesh.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Abstract

Low water availability has increased the use of regulated deficit irrigation strategies in fruit orchards. However, these water restrictions may have implications on fruit growth and quality. The current paper assesses the suitability of an existing fruit tree model (QualiTree) for describing the effects of water stress on peach fruit growth and quality. The model was parameterised and calibrated for a mid-late maturing peach cultivar ('Catherine'). Mean and variability over time of fruit and vegetative growth were consistent with observed data on trees submitted to full irrigation or to regulated deficit irrigation. The relative root mean square errors of the model for growth ranged between 0.09 and 0.31.

Sugar contents in fruit flesh were fairly well simulated, except for sucrose, which was overestimated. The relative root mean square errors of the model ranged from 0.01 to 0.40 for fructose; from 0.04 to 0.05 for glucose; from 0.21 to 0.41 for sucrose and from 0.09 to 0.28 for sorbitol. Water stress reduced leafy shoot growth up to 23% and fruit final size up to 49% when compared to the well-watered control. However, sugar contents in the flesh increased with water stress, up to 70% in the case of glucose. Simulations showed that a severe water stress during stage III of fruit development decreased fruit sizes by 22%, when compared to the control, whereas it enhanced sugar accumulation in the fruit flesh, up to 70% in the case of glucose and fructose. Therefore, these simulations showed that QualiTree might be useful in the design of innovative horticultural practices.

Keywords: *Prunus persica* L. Batsch, fruit quality, reducing sugars, modelling, regulated deficit irrigation, crop production

1. Introduction

Regulated deficit irrigation (RDI) practices are common for peach-tree cultivation in order to save water. This may impose serious water restrictions to the trees. For instance, in Spain, where peach (*Prunus persica* L. Batsch) culture is highly important, restrictions in irrigation water are usually imposed in midsummer, before the harvest of many mid-late

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

maturing cultivars (Lopez et al., 2010); this coincides with the final stage of fruit development (stage III), which is characterized by a high accumulation of fresh and dry weight by the fruit.

Those water restrictions not only may have an effect on fruit size, but also on fruit quality, which is an important issue for fruit production and retailing (Codron et al., 2005). For instance, Berman and DeJong (1996) reported that water stress at stage III limits fruit growth. Hence, marketable fruit size may not be attained. However, other fruit quality criteria could be positively affected, such as soluble solid content in fruit flesh (Crisosto et al., 1994). In this sense, Lopez et al. (2010), studying deficit-irrigated mid-late maturing 'O'Henry' peach, found that RDI significantly increased soluble solid contents. On other species from the *Prunus* genre, such as plum, deficit irrigation has also been reported to increase total soluble solids content in fruits (Intrigliolo and Castel, 2010).

Fruit quality involves a set of traits such as fruit size, overall composition and taste, and proportion of edible tissue (Génard et al., 2009). These traits result from many processes at both the plant and organ levels that show large genotype x environment (management) interactions (Aguirrezábal et al., 2009). Understanding all the interactions between factors affecting fruit quality and the inherent complexity of its build-up is a challenging subject. In this sense, process-based simulation models may be useful tools to discern the complex linked processes controlling fruit size and composition at different levels of organization (Martre et al., 2011). Although several models for simulating fruit-tree functioning have been developed for apple (Costes et al., 2008) and peach (L-PEACH: Allen et al., 2005), accounting for the effect of water stress on carbon partitioning in the latter case (Da Silva et al., 2011), they are not focused on fruit quality. Recently, Lescourret et al. (2011) presented QualiTree, a model that combines physiological and agronomic viewpoints for describing carbon allocation within the tree, vegetative and fruit growth distribution and the development of fruit quality. Because of its parsimony, QualiTree is more convenient than the previous models for quantitative comparison of data for parameterization and evaluation.

In its present state, QualiTree has not been validated with experimental data on sugar concentrations in fruit flesh. Furthermore, the results reported by Mirás-Avalos et al. (2011)

suggest that some parameters within QualiTree are cultivar-dependent. Therefore, the aim of the present work was to validate QualiTree sugar sub-model for a mid-maturing peach tree cultivar (the previous studies were done on early and late maturing cultivars, Mirás-Avalos et al., 2011, 2012) and to use the predictive capabilities of the model for evaluating the effects of water restrictions on fruit and vegetative growth, and also on sugar concentrations in the fruit flesh.

First, QualiTree was parameterised for a mid-maturing peach cultivar (cv. 'Catherine') and validated with observed data from different situations concerning irrigation conditions. The variables considered were the fruit and the leafy shoot dry masses, and the concentrations of four sugars (sucrose, glucose, fructose, and sorbitol) in the fruit. Then, we designed several simulation scenarios to observe the response of the model. Some of these scenarios were theoretical for testing the behaviour of the model and some others were constructed using field observations involving deficit irrigation practices as a basis.

2. Materials and methods

2.1. QualiTree, model overview

QualiTree (Lescourret et al., 2011) is a generic fruit tree model that describes the tree as a set of objects: fruiting units (FU) composed of fruits, leafy shoots and stem wood in a tree architecture, and other compartments viewed globally: old wood (trunk and branches), coarse roots, and fine roots. QualiTree runs, on a daily timestep, from bloom or after bloom until the end of the fruit growing season, starting from an initial state of the tree.

In order to represent the growth in dry mass of all the tree objects, QualiTree uses a carbon-supply approach, allocation rules (priority sequence between processes – e.g., maintenance, then growth – or organs –e.g., leafy shoot growth, then fruit growth; use of reserve as buffers; passive carbon storage), and equations of carbon assimilation (based on leaf area for photosynthesis) and growth requirements (demands). These equations are taken mainly from the FU carbon model of Lescourret et al. (1998).

Briefly, to restore carbon balance within the tree, two main principles are applied. First, the coordination theory (Reynolds and Chen, 1996; Chen and Reynolds, 1997) is used to propose that the imbalance (Im) between leafy shoots and fine roots defined as the ratio of dry structural masses of young shoots and fine roots to the shoot:root ratio at equilibrium (model parameter, SReq) changes the demands of leafy shoots and fine roots. Second, carbon exchanges occur between the tree objects, with proportionality to the supply of the donor, the demands of the recipient and a decreasing effect of geometric distance between donor and recipient objects according to a negative power law. The core of these carbon balance principles lies on three main equations. First, the demands of the stem wood, old wood and coarse root compartments are based on the following equation of potential growth in dry mass (DM, g) according to degree-days (dd):

$$\frac{\Delta DM_x}{\Delta dd} = RGR_x^{ini} DM_x e^{-\theta_\lambda dd} \qquad \text{(Eq. 1)}$$

where subscript x is sw for stem wood, ow for old wood and cr for coarse roots, RGR_x^{ini}, the initial relative growth rate, and θ_λ are parameters (dd^{-1}).

Second, the demands of fruit or leafy shoots of the FU and of fine roots are based on the following equation of potential growth:

$$\frac{\Delta DM_x}{\Delta dd} = RGR_x^{ini}\, \mathrm{Im}^a\, g(dd) DM_x \left(1 - \frac{DM_x}{\mathrm{Im}^a\, DM_x^{\max}}\right) \qquad \text{(Eq. 2)}$$

where subscript x is f for fruit, ls for leafy shoots and fr for fine roots, RGR_x^{ini} (dd^{-1}) is the initial relative growth rate (model parameter), Im (dimensionless) is the imbalance between leafy shoots and fine root masses defined previously, exponent a is 0 for fruit, -1 for leafy shoots and 1 for roots, and $g(dd)$ is defined as:

$g(dd) = 1$ if $dd < dd_{min}$

$g(dd) = \dfrac{dd_{\max} - dd}{dd_{\min} - dd}$ if dd is between dd_{min} and dd_{max}

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

$g(dd) = 0$ if $dd > ddmax$ (Eq. 3)

with dd_{min} and dd_{max} as organ-specific parameters (dd).

DM_f^{max} (g) is the maximum dry mass of a fruit. DM_{ls}^{max} is the product of the leafy shoot number of the FU and the maximum mass of an average individual leafy shoot DM_{ils}^{max}. Respect to the set of fine roots, $\mathrm{DM}_{\mathrm{fr}}^{\max}$ is calculated assuming that its ratio to the maximum mass of leafy shoots on the tree is equal to the shoot:root ratio at equilibrium, SReq:

$$DM_{fr}^{\max} = \frac{N_{ls} DM_{ils}^{\max}}{S\mathrm{Re}q} \quad \text{(Eq. 4)}$$

where N_{ls} is the number of leafy shoots on the tree.

Third, the equation depicting the carbon flow F_{ij} between two object i and j of the tree is:

$$F_{ij} = \frac{ACP_i Demand_j}{\sum_{j=1}^{n} Demand_j} dist_{ij}^{-k} \quad \text{(Eq. 5)}$$

where ACP_i is the available carbon pool of i (gC), i.e., the carbon pool remaining after satisfaction of maintenance respiration (and of leaf growth if i is an FU) from an initial pool made of photosynthates (if i is an FU) and of mobilised reserves, $Demand_j$ (gC) is the carbon demand of j, $dist_{ij}$ (mm) the geometric distance between i and j, n is the total number of objects exchanging carbon and k is a positive parameter (dimensionless). Parameter k expresses the effect of distance on carbon exchange: when k is close to zero, the distance has no effect and carbon is distributed proportionally to carbon demands, whereas high values for k lead to severe effects of distance.

Several fruit quality traits (fruit size, the proportion of the total mass consisting of fruit flesh, dry matter content of the flesh, concentrations of various sugars, and a sweetness index) are also represented by QualiTree.

Fruit sugar content seasonal variation is described as a set of differential equations proposed by Génard et al. (2003):

$$\frac{dM_{su}}{dt} = \lambda_{ph} \frac{dM_{ph}}{dt} - k_1(t) M_{su}$$

$$\frac{dM_{so}}{dt} = (1-\lambda_{ph})\frac{dM_{ph}}{dt} - (k_2 + k_3)M_{so}$$

$$\frac{dM_{gl}}{dt} = \frac{k_1(t)}{2}M_{su} + k_2 M_{so} - k_4(t)M_{gl} - \frac{M_{gl}}{M_{gl}+M_{fr}}\frac{dM_{re}}{dt}$$

$$\frac{dM_{fr}}{dt} = \frac{k_1(t)}{2}M_{su} + k_3 M_{so} - k_4(t)M_{fr} - \frac{M_{fr}}{M_{gl}+M_{fr}}\frac{dM_{re}}{dt}$$

$$k_1(t) = e^{-k_{1.1}*(t-k_{1.2})}$$

$$k_4(t) = k_4\frac{1}{DM}\frac{dDM}{dt} \qquad \text{(Eq. 6)}$$

where M_{su}, M_{so}, M_{gl} and M_{fr} are the amounts of carbon (g) in the form of sucrose, sorbitol, glucose and fructose, respectively; $\frac{dM_{ph}}{dt}$ is the phloem flux of carbon into the fruit; $\frac{dM_{re}}{dt}$ is the amount of carbon used for respiration; DM is the dry mass of fruit flesh; λ_{ph} is the proportion of sucrose in the phloem-sourced sugar pool resulting from plant metabolism; and $k_1(t)$, k_2, k_3 and $k_4(t)$ (day^{-1}) are, respectively, the relative rates of sucrose transformation to glucose and fructose, net sorbitol transformation to glucose, net sorbitol transformation to fructose, and the synthesis of compounds other than sugars from glucose and fructose. $k_1(t)$ decreases over time, and depends on two parameters : $k_{1.1}$ (day^{-1}) which is the relative rate of decrease of $k_1(t)$ and $k_{1.2}$ (day) which is the time at which $k_1(t)$ equals 1 day^{-1}. $k4(t)$ varies during the season like the relative growth rate, with a proportionality factor k_4.

QualiTree variables are subject to change as a result of climate and cultural practices (Mirás-Avalos et al., 2011). Combining QualiTree with a simple light interception model allows one to account for light interception, its alteration during the season through variations of the leaf area density, and the consequences on photosynthesis of each FU (Mirás-Avalos et al., 2011). Briefly, this light interception model predicts radiation interception by a tree, based on the works by Charles-Edwards and Thornley (1973) and de Pury and Farquhar (1997). The tree is within an orchard and its canopy is represented by simple geometric shapes (ellipses).

QualiTree modelises the effect of water stress on the plant development by correcting the rate of light-saturated leaf photosynthesis (Ben Mimoun et al., 1999); this deals directly with source limitation and is accounted for, in the model, through an equation (Harrison et al., 1989) relying the light-saturated leaf photosynthesis to the leaf water potential:

$$P_{\max} = P_{\max 0} \cdot \left(1 - \exp^{\left(B_h\left(A_h + WP^{-1}\right)\right)}\right) \qquad \text{(Eq. 7)}$$

where P_{max} is the potential photosynthesis rate (mmol CO_2 m^{-2} s^{-1}), P_{max0} is the maximal photosynthesis rate (mmol CO_2 m^{-2} s^{-1}) without water stress which depends on the level of reserves in the leaf, A_h and B_h are specific parameters (0.22 MPa^{-1} and 4.43 MPa, respectively), and WP is the leaf water potential.

Furthermore, water management in the fruit obeys a series of equations adapted from Fishman and Génard (1998) in Lescourret and Génard (2005). The effect of irrigation is considered through plant water potential, which plays a major role in these equations.

For a complete list of Qualitree inputs and outputs, see the Electronic Supplementary Material, Tables S1 and S2).

2.2. Experimental data

The experiment concerned a middle-late-maturing cultivar of *Prunus persica* (cv. Catherine). Catherine data were collected in 2008 on a 0.5 ha orchard planted in 1999 at the CEBAS-CSIC experimental station in Fuente Librilla, Murcia, Spain (37º 55' N, 1º 25' W, 360 m altitude). Trees were grafted on GF677 rootstock and planted at 4 m x 6 m spacings on a clay-loam soil. Pest control and fertilization practices were those commonly used by the growers. Trees were hand-thinned 30 days after full-bloom (DAFB), which occurred on March 18. Harvest date was July 1.

Two different irrigation treatments were considered in this study. A full irrigation treatment (FI) where trees were irrigated with enough water to replace 100% of crop

**Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat**

evapotranspiration (ET_c) requirements and a regulated deficit irrigation treatment (RDI) established to adjust a pre-defined threshold of stem water potential (ψ_s) of -1.5 MPa, where a moderate water deficit is applied in a closely controlled way in low stress sensitivity periods (stage II of fruit development defined by a slowing of the diametral growth and stone hardening; Girona et al., 2005). Crop irrigation requirements in FI were determined according to daily crop reference evapotranspiration (ET_0), calculated with the Penman-Monteith equation, a crop factor that varied during the year (Allen et al., 1998) and the percentage of ground area shaded by the tree canopy (Fereres and Goldhamer, 1990). In RDI, applied irrigation doses and frequency were continuously adjusted to match the average pre-defined ψ_s value. The cumulative annual amount of irrigation water for FI and RDI was 750.1 and 460.2 mm, respectively. An experimental design layout is shown in Fig. 1.

Tree water status was assessed through regular measurements (3 days) of leaf (ψ_l) and stem (ψ_s) water potentials. Measurements were performed in two leaves from two trees per replication (i.e. 8 trees per treatment, thus 16 leaves per treatment and measurement date) using a pressure chamber (Soil Moisture Equipment Corp. Model 3000, Santa Barbara, CA, USA). The leaves used for these determinations were mature, healthy and from the north face of the tree near the trunk. For ψ_s measurements, each leaf was individually enclosed in a plastic bag and wrapped in aluminium foil for at least 2 h prior to the measurements. This inhibits leaf transpiration and makes it possible for the water potential in the leaf xylem to be in equilibrium with that of stem xylem at the point of attachment of the petiole.

In FI trees, ψ_s decreased from -0.4 MPa at the beginning of the stage II of fruit growth to -0.7 MPa in stage III, whereas in RDI trees ψ_s ranged between -0.55 and -0.85 MPa during fruit development. In the case of ψ_l, average values for stage II and stage III ranged, respectively from –1.05 to –1.65 MPa for FI trees and from –1.45 to –1.85 MPa for RDI trees. These values were considered in the design of simulation scenarios. Both FI and RDI trees presented the stages of fruit development on the same dates. Stage III of peach fruit development begins when the stone is formed and the fruit starts to grow rapidly again.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Three trees within the orchard were chosen as being representative of these treatments. They are referred to hereinafter as FI Tree 1, FI Tree 2, and RDI. Diameters, lengths of the tree axes, insertion and phyllotaxic angles were measured in order to obtain a description of the tree architecture. FI Tree 1 was used for parameterization purposes and the remaining two trees, namely FI Tree 2 and RDI, were used to test the model.

For these three trees, the diameters (FD, in mm) of all fruits were measured perpendicularly to the fruit suture on each FU using digital callipers. Data were collected every 5-7 days from 57 DAFB until 105 DAFB, when the fruit growth curves displayed a saturation pattern. FD was converted to dry mass (DM, in g) using an allometric relationship derived from experimental data ($DM = 1.7429 \times 10^{-5} \times FD^{3.2654}$, n =143, r^2= 0.96). Leafy shoot length (m) was also measured for each FU four times during fruit growth. Lengths were converted to dry mass (g) using an allometric relationship derived from experimental data (DM = 16.1 x length; n=61).

Randomly, twenty fruits from each treatment were collected on two different dates (66 and 94 DAFB) prior to harvest for sugar analysis. At harvest (105 DAFB), all fruits from each tree were used for sugar analysis. Samples were frozen in liquid nitrogen for preservation before analysis. Soluble sugar (sucrose, glucose, fructose and sorbitol) contents in fruits were determined by high performance liquid chromatography (HPLC) as described by Gomez et al. (2002).

2.3. Input data

Climate data (including global solar radiation and temperature), collected at a weather station located into the experimental field, was used as a model input. Leaf and stem water potential values, for simulating plant water status, were also provided.

Data on diameter and length of the different tree parts at full bloom (i.e., trunk, scaffolds, branches and FU) were used to calculate distances between the virtual tree objects and their initial dry masses as described in Mirás-Avalos et al. (2011). Distances between FUs were calculated according to the pathways between FU on the real tree architecture (Lescourret

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

et al., 2011). For instance, the whole set of distances ranged from 1 to 455 cm in FI Tree 1 (average = 263.3 cm)

The initial dry mass of fine roots was assumed to be proportional to the current-year aboveground parts of the tree (Kozlowski et al., 1991).

Maximum carbon reserve accumulation was defined for each tree compartment as a percentage of its dry mass. Old wood (8%) and coarse roots (8%) carbon reserve values were taken from the works of Jordan and Habib (1996) and Mediene et al. (2002). Reserve values for stems (5.5%) and leafy shoots (16%) at the initial stage of fruit development were obtained from Lescourret and Génard (2005). The list of QualiTree inputs is presented in Table S1 of the Electronic Supplementary Material.

2.4. Estimation of parameters

Some parameters concerning the carbon economy in QualiTree depended on the cultivar (Mirás-Avalos et al., 2011). Table 1 presents the parameters which were estimated in this work. All other parameters were taken from Génard et al. (1998), Lescourret et al. (1998), Lescourret and Génard (2005) and Mirás-Avalos et al. (2011). In the Electronic Supplementary Material, Table S3 presents the complete list of parameters.

Potential fruit and leafy shoot growth parameters, namely the initial relative growth rate (RGR^{ni}), maximal dry mass (DM^{max}), and minimum and maximum degree-days (dd_{min}, dd_{max}) were estimated using non-linear least squares regressions. Data used for this parameterisation consisted of 24 masses for 8 dates corresponding to the higher values in the data set (90% quantile at each date).

The parameters for the sugar submodel were estimated by maximizing likelihood by the Generalized Reduced Gradient method as reported by Génard et al. (2003).

Three parameters were estimated globally by running QualiTree for Catherine: the parameter expressing the effect of distance between tree objects on carbon exchange within the tree (k); the initial relative growth rate of fine roots (RGR_{fr}^{ini}) and that of old wood (RGR_{ow}^{ini}).

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

The value of the initial relative growth rate of coarse roots (RGR_{cr}^{ini}) was considered to be equal to that of the old wood.

The criterion (A) to be minimised for this estimation was a weighted sum of differences averaged over the FU, for the leafy shoot and fruit dry masses:

$$A = \frac{1}{\sigma_y^2}\frac{1}{n}\sum_i\left[\frac{1}{n_i}\sum_{j=1}^{n_i}\left(y_{ij}-y_{ij}^s\right)^2\right]+\frac{1}{\sigma_z^2}\frac{1}{n}\sum_i\left[\frac{1}{n_i}\sum_{j=1}^{n_i}\left(z_{ij}-z_{ij}^s\right)^2\right] \qquad \text{(Eq. 8)}$$

where y_{ij} and z_{ij} are the observed average for leafy shoot and fruit dry mass per FU (i) and per date (j), respectively; y_{ij}^s and z_{ij}^s the corresponding simulated average values of leafy shoot and fruit dry mass per FU (i) and per date (j), respectively; n_i, the number of dates for FU (i); n, the total number of FU; σ_y^2, the variance of y_{ij}; and σ_z^2, the variance of z_{ij}.

2.5. Comparison of observed and simulated values

The observed and simulated values of fruit or leafy shoot dry masses per FU at the same dates were compared using the Relative Root Mean Square Error (RRMSE), a common criterion for evaluating non-linear models (Kobayashi and Salam 2000), here defined as:

$$RRMSE = \frac{1}{\bar{y}}\sqrt{\frac{1}{N}\sum_{i=1}^{N}\left(y_i - y_i^s\right)^2} \qquad \text{(Eq. 9)}$$

where y_i is the observed value, y_i^s the corresponding simulated value, N the number of observed data, and $\bar{y}$ the mean of observed values. This index represents the mean distance between simulation and measurement. The smaller the RRMSE, the more accurate the simulation.

2.6. Simulation scenarios

To test the effects of deficit irrigation and water stress on vegetative and fruit growth, and on fruit sugar development, several simulation scenarios were designed. Water stress scenarios were described through the definition of ψ_l and ψ_s, known to give the plant water status (Choné et al. 2001).

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

A first series of five scenarios aimed at testing the behaviour of the model regarding fruit and leafy shoot growth and sugar concentrations for a range of constant leaf and stem water potential values. Respectively, ψ_l and ψ_s ranged from -0.8 and –0.6 MPa (control) to -3 and -1.3 MPa (very severe stress; Table 2). In these scenarios, water stress began when simulation started. Moreover, four additional scenarios were simulated (Table 2) with a water stress produced either in stage II or in stage III of fruit development, in order to observe the model's response. Those scenarios reproducing a water stress occurring on stage II were divided in three periods of, approximately, two weeks each: from 57 to 75 DAFB, ψ_l and ψ_s were those of non-stress conditions i.e. –0.8 and –0.6 MPa, respectively; from 76 to 89 DAFB, ψ_l and ψ_s were –1.5 and –0.9 MPa (in the case of moderate water stress) and –3.0 and –1.6 MPa (in the case of severe water stress), respectively; from 90 to 105 DAFB (harvest), leaf and stem water potentials were those of non-stress conditions.

Scenarios reproducing water stress during stage III were also built. We maintained ψ_l and ψ_s at –0.8 and –0.6 MPa, respectively, from 57 to 89 DAFB, and then, we decreased ψ_l and ψ_s until harvest to –1.5 and –0.9 MPa for a moderate water stress and to –3.0 and –1.6 MPa for a severe water stress.

These values were chosen from an equation relating three-year data of leaf and stem water potentials for this peach cultivar under the climatic conditions of the studied region (unpublished data).

Other three water stress scenarios were defined considering leaf and stem water potentials reported for peach trees in experimental orchards under different irrigation conditions (e.g., Berman and DeJong, 1996; Besset et al., 2001; Solari et al., 2006; Conejero et al., 2007; López et al., 2008; Mercier et al., 2009; Abrisqueta et al., 2010; Bussi et al., 2010; López et al., 2010). These agronomic scenarios describe three different situations: (i) a control with no water restrictions although the values of water potential fluctuate over the growing period; (ii) a situation of moderate stress, which can be regarded as a scenario of RDI; and (iii) a situation of a severe water stress, which may be due to high water requirements and low water availability.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

The scenarios were analysed by means of analyses of variance using water stress as explaining factor. The output variables were fruit yield in dry mass, fruit average dry mass, total dry mass of leafy shoots, average dry mass of leafy shoots and the concentrations in the fruit flesh of sucrose, glucose, fructose and sorbitol. Tukey's test at 5% level was used for mean separation.

Data analyses were carried out using R software version 2.12.1 (R Development Core Team, 2010).

3. Results

3.1. Parameterisation and test of the model

Parameter values are indicated in table 1. Interestingly, a very low value of the parameter expressing the effect of distance between tree objects on carbon exchange within the tree (*k*) was observed (Table 1). This indicates within-tree distances are not a limitation. It is also worth noting that the rate of sorbitol transformation to fructose (k_3) was greater than that to glucose (k_2) (Table 1).

Simulated leafy shoot dry masses fitted correctly those observed. The variability of the simulated values was similar to that measured in the field (Fig. 2). RRMSE values were 0.09, 0.28, and 0.15 for FI Tree 1, FI Tree 2 and RDI, respectively. These values correspond to the calibration of the model in the case of FI Tree 1 and to the validation of the model in the case of the FI Tree 2 and RDI Tree.

In the case of fruit growth, the simulated patterns of fruit dry masses correctly fitted for FI Tree 1, when predictions were lower than observations on the three last dates for FI Tree 2 (Fig. 2). In RDI tree, there was a good agreement between simulations and observations, except at harvest were the model slightly underestimated the fruit mass. The variability of the observed and simulated values was very similar. The RRMSE values were 0.21, 0.30, and 0.31 for FI Tree 1, FI Tree 2 and RDI, respectively.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Concerning sugar concentrations in the fruit, simulated values at harvest were very similar to those measured except for sucrose, which was clearly overestimated (Fig. 3). The dynamics of sugars in the fruit over the growing season were similar for the three trees considered. In all cases, the variability of simulated values was lower than that of the measurements (Fig. 3). The RRMSE values for glucose, fructose, sucrose and sorbitol were, respectively, 0.04, 0.01, 0.32, 0.09 for FI Tree 1; 0.05, 0.08, 0.21, 0.28 for FI Tree 2; and 0.04, 0.40, 0.41 and 0.13 for RDI Tree.

3.2. Simulation scenarios

Water stress applied during all the season negatively affected both leafy shoot, fruit growth and yield (Fig. 4). In the case of leafy shoots, the decrease in dry mass at harvest between the control scenario and the most stressful conditions (-3 MPa and –1.3 MPa for ψ_l and ψ_s, respectively) was 23%. Fruits were more negatively affected by lower water potential values than leafy shoots, since fruit average dry mass at harvest was 49% lower in the case of a severe water stress than under control conditions (Table 3). The water stress affected positively the four sugars concentrations, with a stronger effect for glucose and fructose (Fig. 4).

The moderate stress has no effect on yield, fruit and leafy shoot mass whatever the stage of application and has a positive effect on sugar concentrations at harvest (Table 4). Severe stress decreases the fruit yield and mass. When applied on stage II it has almost no effect on sugar concentrations whereas it produced significant increases in all sugar concentrations except for sorbitol when applied during stage III (Table 4). It is interesting to note that the stress in stage II had a significant and immediate effect on the concentrations of glucose and fructose, but this effect disappeared quickly when the stress stopped (Fig. 5).

When considering water stress scenarios close to real conditions, yield and fruit average dry mass at harvest were significantly affected by severe water stress. In contrast, leafy shoot total and average masses were not significantly influenced by water stress (Fig 6). Regarding sugar concentrations in fruit (Table 5), a severe water stress produced higher concentrations of the four sugars accounted (sucrose, glucose, fructose and sorbitol); whereas a moderate water

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

stress significantly increased the concentrations of sucrose, glucose and fructose but not that of sorbitol (Fig 6).

4. Discussion

A middle-late maturing peach cultivar ('Catherine') was successfully implemented and parameterised into QualiTree, a virtual tree model (Lescourret et al. 2011) that simulates the within-tree variations in fruit and leafy-shoot dry masses. The parameterization of this middle-late maturing peach cultivar broadened the predictive capacities of the model, since certain parameters within QualiTree are cultivar dependent (Mirás-Avalos et al. 2011, 2012). Several parameters differed in this cultivar compared to those of extra-early, early and late maturing peach cultivars ('Flordastar', 'Alexandra' and 'Suncrest', respectively). The initial relative growth rates of fruits and leafy shoots were, in 'Catherine', intermediate between those reported for 'Alexandra' and 'Suncrest'. The same was observed for the maximal dry weight of fruits (for a complete set of parameters for 'Alexandra' and 'Suncrest' cultivars see Mirás-Avalos et al. 2011). Moreover, the parameter expressing the effect of distance between tree objects on carbon exchange within the tree (*k*, see Lescourret et al. 2011) was very low, indicating that within-tree distances were not limiting as was observed for 'Flordastar', 'Alexandra' and 'Suncrest' (Mirás-Avalos et al. 2011, 2012). This agrees with field data reported by Lopez et al. (2007). Furthermore, a novel advance in the model issued from the current work is the parameterisation for four sugars (glucose, fructose, sucrose and sorbitol) enhancing the predictive capabilities of QualiTree since now it is able to offer information on fruit quality as well as on fruit size.

QualiTree also reproduced satisfactorily the observed fruit and leafy shoot growth of a peach tree cv. 'Catherine' subject to water stress, a major factor affecting fruit and vegetative growth (Mercier et al. 2009; Lopez et al. 2010), even though the model evaluation did not consider the possible heterogeneity of leaf response to water stress due to a high variability of irradiation within the canopy (Díaz-Espejo et al., 2007). The model was also capable of reproducing the observed concentrations of four sugars (sucrose, fructose, glucose and sorbitol),

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

in the fruit flesh. However, sucrose was overestimated in both FI and RDI trees and fructose was overestimated under RDI conditions, suggesting that further improvements are necessary.

Simulation scenarios allowed us to observe that, for a middle-late maturing peach cultivar ('Catherine'), significant reductions in fruit size appeared at ψ_l of –2 MPa. However, leafy shoots were less sensitive to water stress than fruits, as they were significantly affected only by ψ_l lower than –2.5 MPa.

In contrast, all the sugar concentrations increased continuously with the water stress when it is applied from the beginning of the simulation. However, it does not predict a higher sensitivity of sorbitol than sucrose, which is not in agreement with the results of Lo Bianco et al. (2000).

Simulation results are in accordance with several field studies that reported an enhancement of fruit quality under RDI conditions. For instance, Crisosto et al. (1994) and Intrigliolo and Castel (2010) observed that deficit irrigation increased total soluble solids content in fruits. Besset et al (2001) observed a greater content in total soluble solids in fruits from peach trees under water stress conditions when compared to fully irrigated trees. These results also agreed with data reported by Intrigliolo and Castel (2010) for prunes, as they observed an improvement in fruit composition in trees under regulated deficit irrigation conditions. In addition, Barry et al. (2004) observed, in citrus, that withholding water from trees during stage II of fruit development increased the concentrations of fructose and glucose. Moreover, sorbitol, glucose and fructose have been reported to be partitioned according to the relative size of the fruit (Lo Bianco and Rieger, 2002). Thus, taking into account that irrigation affects fruit final size (Bryla et al., 2005; Lopez et al., 2011), sugar concentrations in fruit flesh may also be affected. In view of the results from our simulations, QualiTree may provide useful information on sugar contents in fruit flesh.

Our results validate the fact that RDI strategies allow the maintenance or even enhancement of fruit quality while saving water as suggested by several field studies (Besset et al., 2001; Fereres and Soriano, 2007; Intrigliolo and Castel, 2010; Lopez et al., 2011).

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

The simulations allowed us to observe what would happen when trees were imposed to different levels of water stress two weeks before fruit harvest. This period is critical for final fruit size. According to QualiTree, no significant effects were observed on fruit yield when water stress was moderate (-0.9 and –1.5 MPa for ψ_s and ψ_l, respectively) but significant increases in sucrose, glucose, fructose and sorbitol in fruit flesh were detected. However, when a severe water stress (-1.6 and –3 MPa for ψ_s and ψ_l, respectively) occurred, significant reductions in fruit yield (22% less than under control conditions) were predicted and they may not be compensated by the increase in sugar contents in the fruit flesh. The results of our simulations are in accordance with other simulation studies (Génard et al. 2009).

Acknowledgements. We are grateful to the IRRIQUAL (EU-FP6-FOOD-CT-2006-023120) and SIRRIMED (KBBE-2009-1-2-03, PROPOSAL Nº 245159) projects for financial support. We also acknowledge two SENECA projects (05665/PI/07 and 11872/PI/09) and CONSOLIDER INGENIO 2010 (MEC CSD2006-0067) and CICYT (AGL2010-17553) projects for funding this research. J.M. Mirás-Avalos thanks Xunta de Galicia for funding his contract within the framework of the program "Isidro Parga Pondal".

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Inputs for QualiTree

Table S2. Ouputs from QualiTree

Table S3. Parameter values concerning carbon economy and fruit quality in QualiTree

References

Abrisqueta, I., Tapia, L.M., Conejero, W., Sánchez-Toribio, M.I., Abrisqueta, J.M., Vera, J., Ruiz-Sanchez, M.C., 2010. Response of early-peach [*Prunus persica* (L.)] trees to deficit irrigation. Span. J. Agric. Res. 8(S2), S30-S39.

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Aguirrezábal, L.A.N, Martre, P., Pereyra-Irujo, G., Izquierdo, N., Allard, V., 2009. Management and breeding strategies for the improvement of grain and fruit quality. In: Sadras, V.O., Miralles, D.J. (eds.). Crop physiology: Applications for genetic improvement and agronomy. San Diego, CA, USA. Academic Press, 387-421.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration – guidelines for computing crop water requirements. Irrigation and Drainage 56, FAO, Rome, 300 p.

Allen, M.T., Prusinkiewicz, P., DeJong, T.M., 2005. Using L-systems for modelling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. New Phytol. 166(3): 869-880.

Barry, G.H., Castle, W.S., Davies, F.S., 2004. Rootstocks and plant water relations affect sugar accumulation of citrus fruit via osmotic adjustment. J. Amer. Soc. Hort. Sci. 129(6), 881-889.

Ben Mimoun, M., Lescourret, F., Génard, M., 1999. Modeling carbon allocation in peach shoot bearing fruits: simulation of the water stress effect. Fruits 54, 129-134.

Berman, M.E., DeJong, T.M., 1996. Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*). Tree Physiol. 16, 859-864.

Berman, M.E., DeJong, T.M., 2003. Seasonal patterns of vegetative growth and competition with reproductive sinks in peach (*Prunus persica*). J. Horticult. Sci. Biotechnol. 78(3), 303-309.

Besset, J., Génard, M., Girard, T., Serra, V., Bussi, C., 2001. Effect of water stress applied during the final stage of rapid growth on peach trees (cv. Big-Top). Sci. Hortic. 91, 289-303.

Bryla, D.R., Dickson, E., Shenk, R., Scott Johnson, R., Crisosto, C.H., Trout, T.J., 2005. Influence of irrigation method and scheduling on patterns of soil and tree water status and its relation to yield and fruit quality in peach. HortScience 40(7), 2118-2124.

Bussi, C., Lescourret, F., Mercier, V., Génard, M., 2010. Effects of winter pruning and of water restriction on fruit and vegetative growth, water potential and leaf gas exchange during

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

the final stage of rapid growth in an early maturing peach cultivar. Europ. J. Hort. Sci. 75(1), 15-19.

Charles-Edwards, D.A., Thornley, J.H.M., 1973. Light interception by an isolated plant. A simple model. Ann. Bot. 37, 919-928

Chen, J.L., Reynolds, J.F., 1997. A coordination model of whole-plant carbon allocation in relation to water stress. Ann. Bot. 80(1), 45-55.

Choné, X., van Leeuwen, C., Dubourdieu, D., Gaudillère, J.P., 2001. Stem water potential is a sensitive indicator of grapevine water status. Ann. Bot. 87, 477-483.

Codron, J.M., Giraud-Heraud, E., Soler, L.G., 2005. Minimum quality standards, premium private labels, and European meta and fresh produce retailing. Food Policy 30, 270-283.

Conejero, W., Alarcón, J.J., García-Orellana, Y., Nicolás, E., Torrecillas, A., 2007 Evaluation of sap flow and trunk diameter sensors for irrigation scheduling in early maturing peach trees. Tree Physiol. 27, 1753-1759.

Costes, E., Smith, C., Renton, M., Guedon, Y., Prusinkiewicz, P., Godin, C., 2008. MApple-T: simulation of apple tree development using mixed stochastic and biomechanical models. Funct. Plant Biol. 35(9-10): 936-950.

Crisosto, C.H., Scott Johnson, R., Luza, J.G., Crisosto, G.M., 1994. Irrigation regimes affect fruit soluble solids concentration and rate of water loss of ‘O’Henry’ peaches. HortScience 29(10), 1169-1171.

Da Silva, D., Favreau, R., Auzmendi, I., DeJong, T.M., 2011. Linking water stress effects on carbon partitioning by introducing a xylem circuit into L-PEACH. Ann. Bot. 108, 1135-1145.

de Pury, D.G.G., Farquhar, G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ. 20, 537-557.

Díaz-Espejo, A., Nicolás, E., Fernández, J.E., 2007. Seasonal evolution of diffusional limitations and photosynthetic capacity in olive under drought. Plant Cell Environ. 30, 922-933.

Fereres, E., Goldhamer, D.A., 1990. Deciduous fruit and nut trees, in: Stewart, B.A., Nielsen, D.R. (Eds.), Irrigation of Agricultural Crops. A.S.A. Madison, WI, Monograph 30, pp. 987-1017.

Fereres, E., Soriano, M.A., 2007. Deficit irrigation for reducing agricultural water use. J. Exp. Bot. 58, 147-159.

Fishman, S., Génard, M., 1998. A biophysical model of fruit growth: simulation of seasonal and diurnal dynamics of mass. Plant Cell Environ. 21(8), 739-752.

Génard, M., Lescourret, F., Ben Mimoun, M., Besset, J., Bussi, C., 1998. A simulation model of growth at the shoot-bearing fruit level. II. Test and effect of source and sink factors in the case of peach. Eur. J. Agron. 9, 189-202.

Génard, M., Lescourret, F., Gomez, L., Habib, R., 2003. Changes in fruit sugar concentrations in response to assimilate supply, metabolism and dilution: a modeling approach applied to peach fruit (*Prunus persica*). Tree Physiol. 23, 373-385.

Génard, M., Gibert, C., Bruchou, C., Lescourret, F., 2009. An intelligent virtual fruit model focusing on quality attributes. J. Hortic. Sci. Biotecnol. SI, 157-163.

Girona, J., Gelly, M., Mata, M., Arbonès, A., Rufat, J., Marsal, J., 2005. Peach tree response to single and combined deficit irrigation regimes in deep soils. Agr. Water Manage. 72:97-108.

Gomez, L. Rubio, E., Augé, M., 2002. A new procedure for extraction and measurement of soluble sugars in ligneous plants. J. Sci. Food Agric. 82, 360-369.

Grossman, Y.L., DeJong, T.M., 1994. Carbohydrate requirements for dark respiration by peach vegetative organs. Tree Physiol. 14, 37-48.

Harrison, R.D., Daniell, J.W., Cheshire, J.M., 1989. Net photosynthesis and stomatal conductance of peach seedlings and cutting in response to changes in soil water potential. J. Am. Soc. Hortic. Sci. 114, 986-990.

Hipps. N.A., Pagès, L., Huguet, J.G., Serra, V., 1995. Influence of controlled water suplí on shoot and root development of young peach trees. Tree Physiol. 15, 95-103.

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Intrigliolo, D.S., Castel, J.R., 2010. Response of plum trees to deficit irrigation under two crop levels: tree growth, yield and fruit quality. Irrig. Sci. 28, 525-534.

Jordan, M.O., Habib, R., 1996. Mobilizable carbon reserves in young peach trees as evidenced by trunk girdling experiments. J. Exp. Bot. 47, 79-87.

Kobayashi, K., Salam, M.U., 2000. Comparing simulated and measured values using mean squared deviation and its components. Agron. J. 92, 345-352.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA, 657 p.

Lescourret, F., Ben Mimoun, M., Génard, M., 1998. A simulation model of growth at the shoot-bearing fruit level. I. Description and parameterization for peach. Eur. J. Agron. 9, 173-188.

Lescourret, F., Génard, M., 2005. A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth. Tree Physiol. 25, 1303-1315.

Lescourret, F., Moitrier, N., Valsesia, P., Génard, M., 2011. QualiTree, a virtual fruit tree to study the management of fruit quality. I. Model development. Trees Struc. Func. 25, 519-530.

Lo Bianco, R., Rieger, M., Sung, S.J.S., 2000. Effect of drought on sorbitol and sucrose metabolism in sinks and sources of peach. Physiologia Plantarum 108, 71-78.

Lo Bianco, R., Rieger, M., 2002. Partitioning of sorbitol and sucrose catabolism within peach fruit. J. Amer. Soc. Hort. Sci. 127(1), 115-121.

Lopez, G., Girona, J., Del Campo, J., Marsal, J., 2007. Effects of relative source-sink position within peach trees on fruit growth under water stress conditions. J. Hortic Sci. Biotechnol. 82 (1), 140-148.

Lopez, G., Behboudian, M.H., Vallverdu, X., Mata, M., Girona, J., Marsal, J., 2010. Mitigation of severe water stress by fruit thinning in 'O'Henry' peach: Implications for fruti quality. Sci. Hortic. 125, 294-300.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Lopez, G., Behboudian, M.H., Echeverria, G., Girona, J., Marsal, J., 2011. Instrumental and sensory evaluation of fruit quality for 'Ryan's Sun' peach grown under déficit irrigation. HortTechnology 21, 712-719.

Martre, P., Bertin, N., Salon, C., Génard, M., 2011. Modelling the size and composition of fruit, grain and seed by process-based simulation models. New Phytol. 191, 601-618.

Mediene, S., Jordan, M.O., Pagès, L., Lebot, J., Adamovicz, S., 2002. The influence of severe shoot pruning on growth, carbon and nitrogen status in young peach trees (*Prunus persica*). Tree Physiol. 22, 1289-1296.

Mercier, V., Bussi, C., Lescourret, F., Génard, M., 2009. Effects of different irrigation regimes applied during the final stage of rapid growth on an early maturing peach cultivar. Irrig. Sci. 27, 297-306.

Mirás-Avalos, J.M., Egea, G., Nicolás, E., Génard, M., Vercambre, G., Moitrier, N., Valsesia, P., González-Real, M.M., Bussi, C., Lescourret, F., 2011. QualiTree, a virtual fruit tree to study the management of fruit quality. II. Parameterisation for peach, analysis of growth-related processes and agronomic scenarios. Trees Struct. Funct. 25, 785-799.

Mirás-Avalos, J.M., Alcobendas, R., Alarcón, J.J., Pedrero, F., Valsesia, P., Lescourret, F., Nicolás, E., 2012. Combined effects of water stress and fruit thinning on fruit and vegetative growth of a very-early maturing peach cultivar: assessment by means of a fruit tree model, QualiTree. Irrig. Sci. doi: 10.1007/s00271-012-0385-6

R Development Core Team, 2010. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org/.

Reynolds, J.F., Chen, J.L., 1996. Modelling whole-plant allocation in relation to carbon and nitrogen supply: coordination versus optimization: opinion. Plant Soil 185(1), 65-74.

Rieger, M., Marra, F., 1994. Responses of young peach trees to root confinement. J. Am. Soc. Hortic. Sci. 119, 223-228.

Solari, L.I., Johnson, S., DeJong, T.M., 2006. Relationship of water status to vegetative growth and leaf gas exchange of peach (*Prunus persica*) trees on different rootstocks. Tree Physiol. 26, 1333-1341.

Tables

Table 1. Parameter values concerning carbon economy and sugar development in QualiTree for cv. 'Catherine'.

Parameter	Definition (corresponding equation)	Unit	Value	Origin
Global parameters				
SReq	Shoot:root ratio at equilibrium (Eq. 4)	Dimensionless	4.6	Grossman and DeJong (1994); Rieger and Marra (1994), Hipps et al. (1995), Mediene et al. (2002)
K	Parameter expressing the effect of distance between organs on carbon exchange within the tree (Eq. 5)	Dimensionless	0.002	This work
Specific parameters for leafy shoots				
dd_{min}	Minimum degree-day value (Eq. 3)	degree-days	600	This work
dd_{max}	Maximum degree-day value (Eq. 3)	degree-days	2800	This work
RGR_{ls}^{ini}	Leafy shoot initial relative growth rate (Eq. 2)	degree-days^{-1}	2×10^{-3}	This work
DM_{ls}^{max}	Leafy shoot maximal dry mass (Eq. 2)	g	66	This work
Specific parameters for fruits				
dd_{min}	Minimum degree-day value (Eq. 3)	degree-days	600	This work
dd_{max}	Maximum degree-day value (Eq. 3)	degree-days	3500	This work
RGR_{f}^{ini}	Fruit initial relative growth rate (Eq. 2)	degree-days^{-1}	37×10^{-4}	This work
DM_{f}^{max}	Potential dry mass of fruits at maturity (Eq. 2)	g	55	This work
Growth for different structural parts				
RGR_{ow}^{ini}	Old wood and coarse root initial relative growth rate (Eq. 1)	degree-days^{-1}	4×10^{-4}	Mirás-Avalos et al. (2011)
RGR_{fr}^{ini}	Fine root initial relative growth rate (Eq. 2)	degree-days^{-1}	0.04	This work
RGR_{sw}^{ini}	Stem wood initial relative growth rate (Eq. 1)	degree-days^{-1}	7×10^{-4}	Berman and DeJong (2003)
Partitioning of carbon flow from the phloem into sugars				
λ_{ph}	Proportion of carbon as sucrose in the phloem sap (Eq. 6)	Dimensionless	0.48	This work
$k_{1,1}$	Relative rate of decrease of $k_{1(t)}$ (Eq. 6)	day^{-1}	0.12	Génard et al. (2003)
$k_{1,2}$	Time at which $k_{1(t)} = 1$ day^{-1} (Eq. 6)	day	65	This work
k_2	Relative rate of sorbitol transformation to glucose (Eq. 6)	day^{-1}	0.42	This work
k_3	Relative rate of sorbitol transformation to fructose (Eq. 6)	day^{-1}	0.6	This work
k_4	Ratio of the relative rate of glucose and fructose transformation to the relative growth rate (Eq. 6)	Dimensionless	2.5	This work
Water stress on photosynthesis				
A_h	(Eq. 7)	MPa^{-1}	0.22	Harrison et al., 1989
B_h	(Eq. 7)	MPa	4.43	Harrison et al., 1989
Duration of the different phenological stages				
I	Beginning of Stage I of fruit development	DAFB	18	Field data
II	Beginning of Stage II of fruit development	DAFB	49	Field data
III	Beginning of Stage III of fruit development	DAFB	76	Field data
H	Harvest	DAFB	105	Field data

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Table 2. Water stress scenarios.

Type	Water stress scenario	Starting date (DAFB)	Leaf water potential (MPa)	Stem water potential (MPa)
Theoretical	Control	57	-0.8	-0.6
	Stress 1	57	-1.5	-0.9
	Stress 2	57	-2.0	-1.0
	Stress 3	57	-2.5	-1.2
	Stress 4	57	-3.0	-1.3
	Stress in stage II	57	-0.8	-0.6
		76	-1.5	-0.9
		90	-0.8	-0.6
	Stress in stage III	57	-0.8	-0.6
		90	-1.5	-0.9
	Severe stress in stage II	57	-0.8	-0.6
		76	-3.0	-1.6
		90	-0.8	-0.6
	Severe stress in stage III	57	-0.8	-0.6
		90	-3.0	-1.6
Agronomic	Control	57	-0.6	-0.3
		76	-1.2	-0.6
		90	-1.8	-0.9
	Moderate stress	57	-0.8	-0.4
		76	-1.8	-0.9
		90	-2.6	-1.3
	Severe stress	57	-1.0	-0.5
		76	-2.6	-1.3
		90	-3.0	-2.0

Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Table 3. Mean values at harvest (DAFB = 105) for yield, fruit and shoot dry mass and concentrations of sucrose, glucose, fructose and sorbitol according to the theoretical water stress scenarios. Significant differences are indicated. Values correspond to dry mass and grams of the corresponding sugar per gram of fruit fresh mass.

Scenario	Dry mass (g)				Concentration (g g fresh mass^{-1})			
	Yield (g/FU)	Fruit average mass	Leafy shoot total mass (g/FU)	Leafy shoot average mass	Sucrose	Glucose	Fructose	Sorbitol
Control	23.65^{b}	19.70^{d}	155.20^{a}	15.01^{b}	0.049^{a}	0.010^{a}	0.013^{a}	0.0030^{a}
Stress 1	22.41^{b}	18.68^{cd}	149.48^{a}	14.46^{b}	0.060^{b}	0.012^{b}	0.016^{b}	0.0035^{b}
Stress 2	19.99^{ab}	16.67^{c}	141.23^{a}	13.67^{ab}	0.062^{c}	0.013^{c}	0.017^{c}	0.0036^{b}
Stress 3	16.25^{ab}	13.54^{b}	130.80^{a}	12.66^{ab}	0.066^{d}	0.014^{d}	0.020^{d}	0.0039^{c}
Stress 4	12.44^{a}	10.35^{a}	119.36^{a}	11.56^{a}	0.063^{c}	0.016^{e}	0.021^{e}	0.0038^{c}

Different letters in the columns indicate significant differences at α=0.05.

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

Table 4. Mean values at harvest (DAFB = 105) for yield, fruit and shoot dry mass and concentrations of sucrose, glucose, fructose and sorbitol according to the theoretical water stress scenarios with two times of occurrence. Significant differences are indicated. Values correspond to dry mass and grams of the corresponding sugar per gram of fruit fresh mass.

Scenario	Dry mass (g)				Concentration (g g fresh mass^{-1})			
	Yield (g/FU)	Fruit average mass	Leafy shoot total mass (g/FU)	Leafy shoot average mass	Sucrose	Glucose	Fructose	Sorbitol
Control	23.65^{b}	19.70^{b}	155.20^{a}	15.01^{a}	0.049^{a}	0.010^{a}	0.013^{a}	0.0030^{a}
Stress in stage II	23.42^{b}	19.52^{b}	153.39^{a}	14.84^{a}	0.061^{b}	0.012^{b}	0.016^{b}	0.0037^{b}
Stress in stage III	23.21^{b}	19.35^{b}	153.97^{a}	14.89^{a}	0.059^{b}	0.012^{b}	0.016^{b}	0.0034^{b}
Severe stress in stage II	19.84^{ab}	16.52^{a}	142.79^{a}	13.82^{a}	0.050^{a}	0.010^{a}	0.013^{a}	0.0035^{b}
Severe stress in stage III	18.44^{a}	15.36^{a}	146.77^{a}	14.20^{a}	0.061^{b}	0.017^{c}	0.023^{c}	0.0029^{a}

Different letters in the columns indicate significant differences at α=0.05.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Table 5. Mean values at harvest (DAFB = 105) for yield, fruit and shoot dry mass and concentrations of sucrose, glucose, fructose and sorbitol according to the agronomic water stress scenarios. Significant differences are indicated. Values correspond to dry mass and grams of the corresponding sugar per gram of fruit fresh mass.

Scenario	Dry mass (g)				Concentration (g g fresh mass^{-1})			
	Yield (g/FU)	Fruit average mass	Leafy shoot total mass (g/FU)	Leafy shoot average mass	Sucrose	Glucose	Fructose	Sorbitol
Control	22.69^{b}	18.92^{c}	152.42^{a}	14.74^{a}	0.058^{a}	0.012^{a}	0.016^{a}	0.0032^{a}
Moderate stress	19.65^{ab}	16.39^{b}	145.73^{a}	14.10^{a}	0.066^{b}	0.016^{b}	0.021^{b}	0.0034^{a}
Severe stress	16.53^{a}	13.77^{a}	137.36^{a}	13.29^{a}	0.082^{c}	0.023^{c}	0.030^{c}	0.0044^{b}

Different letters in the columns indicate significant differences at $\alpha=0.05$.

**Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat**

Figures

Figure 1. Experimental design layout of the field experiment. The coloured trees were implemented in QualiTree.

Figure 2. Test of the model against experimental data for the three Catherine trees analysed (FI tree 1, FI tree 2, and RDI tree) under different conditions. Variation of leafy shoot growth and fruit growth among monitored shoots (mean ± SD) according to DAFB, either observed (black squares and black lines) or simulated (white circles and dotted lines). The total number of FU (n) is indicated on each plot. Results from FI tree 1 corresponded to the calibration of the model, whereas those from FI tree 2 and RDI tree refer to the validation of the model.

Figure 3. Test of the model against experimental data for the three Catherine trees analysed (FI tree 1, FI tree 2 and RDI tree). Variation of sugar concentrations among monitored fruits (mean ± SD) according to DAFB, either observed (black squares and black lines) or simulated (white circles and dotted lines). The total number of FU (n) is indicated on each plot. Results from FI tree 1 corresponded to the calibration of the model, whereas those from FI tree 2 and RDI tree refer to the validation of the model.

Figure 4. Simulation of the effect of different leaf and stem water potentials (expressed in MPa) on leafy shoot (LS) and fruit growth in dry mass, and on the concentrations in the fruit flesh of four reducing sugars according to days after bloom. See the description of theoretical water stress scenarios for further details.

Figure 5. Simulation of the effect of two levels and application times of water stress on sugar concentrations in the fruit according to days after bloom. The change in the leaf and stem water potentials (expressed in MPa) occurs at 76 days after bloom (stage II of fruit development) or at

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008

Agricultural Water Management (2013), Vol. 128, p. 1-12, DOI: 10.1016/agwat.2013.06.008,
Journal homepage: http://www.elsevier.com/locate/agwat

90 days after bloom (stage III of fruit development). See the description of theoretical water stress scenarios for further details.

Figure 6. Simulation of the effect of different agronomic scenarios (see the text for further details) on the leafy shoot (LS) total and average dry masses, fruit yield, fruit average dry mass, and on the concentrations in the fruit flesh of four sugars according to days after bloom.

Comment citer ce document :
Miras Avalos, J. M. (Auteur de correspondance), Alcobendas, R. ., Alarcón, J. J. ., Valsesia, P., Génard, M., Nicolás, E. (2013). Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agricultural Water Management, 128, 1-12. DOI : 10.1016/agwat.2013.06.008