# Developing a Physiological Basis for Modeling Peach Canopy Photosynthesis under Water Stress Conditions

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## Abstract

**Daily leaf photosynthesis was reported to be linearly related with daily leaf PAR (photosynthetic active radiation) interception, in peach trees. This relationship was considered as a fundamental step for modeling whole peach canopy photosynthesis. However, data reporting linear relationships was obtained under non-water-stressed trees. Although commercial peach orchards are usually managed under full irrigation, reduced irrigation might become inevitable in water limited areas. Water shortage is becoming increasingly frequent in peach producing areas with Mediterranean climates. Modeling the effect of water stress, on whole canopy photosynthesis, requires studies on the effect of water stress on the relationship between daily leaf photosynthesis and daily leaf light interception. We, therefore, studied the effects of water stress on the linear relationship between daily photosynthesis and light interception in a commercial 'Ryan's Sun' peach orchard. Water stress was imposed during the final stage of fruit development (50 days before harvest), because irrigation restrictions usually occur mid-summer. Under full irrigation conditions, there was a linear relationship between daily intercepted PAR and daily photosynthetic $CO_2$ assimilation. This relationship had approximately a zero y-intercept. Under water stress conditions, the y-intercept was maintained, but there was a significant decrease in daily photosynthetic $CO_2$ assimilation rates, at high levels of daily intercepted PAR. The higher the level of water stress, the higher the reduction in $CO_2$ assimilation. The main consequence is that linearity between daily intercepted PAR and daily photosynthetic $CO_2$ assimilation was not maintained under severe water stress conditions. Photosynthetic radiation use efficiency (PhRUE), for all leaves of the canopy, was similar under full irrigation conditions. However, under water stress conditions, the leaves that intercepted high values of PAR had significantly reduced PhRUE. These results can facilitate modeling the effect of water stress on whole canopy photosynthesis, in peach trees.**

## INTRODUCTION

Deciduous tree canopies consist of a gradient of leaves exposed to different light environments during the day and, consequently, leaves differ in their photosynthetic activity (DeJong and Doyle, 1985). Under field conditions, linear positive relationships between daily leaf photosynthesis (dPn) and daily leaf intercepted photosynthetically active radiation (dIPAR) was described in peaches (Rosati et al., 2002), almonds and walnuts (Rosati et al., 2004). Another characteristic of the dPn and dIPAR relationship is the zero intercept. Linearity and zero intercept, in the relationship between dPn and dIPAR, implies that all leaves of the canopy have similar photosynthetic radiation use efficiency (PnRUE) (Rosati and DeJong, 2003; Rosati et al., 2004). If the canopy is simplified as a big leaf, daily canopy photosynthesis can be easily estimated from canopy light interception and PnRUE data (Rosati et al., 2004). This approach was considered as a fundamental step for modeling whole-canopy photosynthesis in deciduous fruit trees (Rosati et al., 2002, 2004), simplifying methodological problems derived from its determination (Corelli Grapadelli, 2003).

The simple method to estimate tree canopy photosynthesis, based on daily leaf

PnRUE properties and canopy light interception, is attractive but has some limitations. As pointed out by Rosati et al. (2004), this method is only valid under conditions of no environmental stresses. However, under field conditions, fruit trees are subjected to many environmental stresses. Among them, water stress is one of the most important in fruit producing areas with Mediterranean climates. It is well known that leaf photosynthesis is reduced under water stress, due to stomatal closure and reduced mesophyll conductance (Flexas et al., 2006). However, not all leaves within the canopy respond equally to water stress and, consequently, photosynthetic capacity distribution in the canopy may not be related to light exposure (Diaz-Espejo et al., 2007). Niinemets (2007) reported that leaves exposed to high irradiance may suffer from greater water stress than leaves exposed to low irradiance. If so, water stress could curb the relationship between dPn and dIPAR, described by Rosati et al. (2002, 2004), and reduce daily PnRUE for leaves exposed to high irradiance levels. To test this hypothesis, we studied the effects of water stress on dPn and dIPAR relationships, in peach trees, using a similar approach to that developed by Rosati et al. (2002, 2004). No irrigation was applied during Stage III (50 days before harvest), in a commercial 'Ryan's Sun' peach orchard.

## MATERIAL AND METHODS

### Experimental Orchard

The experiment was conducted in 2010 at a commercial peach (*Prunus persica* L. Batsch 'Ryan's Sun') orchard located in Alcarràs, Lleida, Spain. The trees were 11 years old and were grafted onto GF-677® INRA rootstock. They were planted 3 m apart, in rows 5 m apart, in a north-south orientation to 15° east of north. Trees were trained to an open vase system with four primary scaffolds. Two primary scaffolds were oriented to the east and the other two to the west. Primary scaffolds had an angle of about 45°, and all of them were connected at a trunk height of about 50 cm. Maximum tree height was about 3 m. Fruits were harvested on 3 dates (August 27, September 3 and 8). Crop load was about 375 fruits per tree.

### Irrigation Management and Treatments

Trees were irrigated, on a daily basis, by a drip irrigation system, with 6 drippers per tree (2.2 L $h^{-1}$ per dripper), as described by Lopez et al. (2008a). All trees received full irrigation (100% of ETc), from fruit set until the onset of Stage III of fruit development (50 days before harvest). Then, 2 irrigation treatments were applied: full irrigation (FI) and no irrigation (NI). A randomized complete block design, with 3 block replicates, was used. Each block housed the 2 treatments in different plots. Each plot had 4 rows of 5 trees. The 6 central trees of the middle rows were used as experimental trees, and all the others as guard trees. We, therefore, monitored 36 trees.

The amount of water applied in each plot was measured with digital water meters (CZ2000-3M, Contazara, Zaragoza, Spain). Mid-day stem water potential (SWP) was measured twice a week, during Stage III, using a pressure chamber (Model 3005, Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Measurements were taken at solar noon from leaves located near the base of the trees (one leaf per tree). We monitored 3 and 6 trees per plot, in the FI and NI treatments, respectively. The effects of the treatments on SWP were evaluated by analysis of variance (ANOVA), using the SAS 9.2 software package (SAS Institute, Cary, NC). Statistical significance was established. LSD test was used to separate least square means that differed significantly.

### Leaf Light Interception and Photosynthesis

The daily course of leaf incident PAR was determined at the onset of Stage III, using a quantum PAR sensor (LI-COR 190SA, Lincoln, NE, USA) connected to a portable datalogger (LI-COR 1400, Lincoln, NE, USA). The quantum PAR sensor was mounted in the extreme of a hand-held 2-m stick and was connected to a datalogger with a 3-m cable. Sixty fully mature leaves (15 leaves per scaffold) distributed homogeneously within the whole canopy were tagged in order to have a broad range of leaf incident PAR values, in 2 FI and NI trees. Within a given scaffold, groups of 3 leaves were located at different tree heights (250, 200, 150, 100 and 50 cm). When incident PAR above the canopy exceeded 200 µmol $m^{-2}$ $s^{-1}$ (from approximately dawn to sunset), leaf incident PAR of tagged leaves was measured on a 2-h basis (7 measurements). dIPAR, for the 60 leaves within the canopy, was calculated by integrating hourly data from the daily course of leaf incident PAR.

Leaves were then categorized as shade and sun leaves, based on their dIPAR values. Shade leaves were those with dIPAR values lower than 5 mol $m^{-2}$ $day^{-1}$. Photosynthetic light response (Pn-light) curves were determined for mature shade and sun leaves, for trees with different SWP values, during Stage III (2 to 3 leaves per tree). Pn-light curves were obtained using a portable LI-6400 infrared gas analyser (LI-COR 6400, Lincoln, NE, USA) supplied with a leaf chamber fluorometer (LI-COR 6400-40, Lincoln, NE, USA) integrated with a LED light source. We modified light intensity, from high PAR values (2000 µmol PAR $m^{-2}$ $s^{-1}$) to low PAR values (0 µmol PAR $m^{-2}$ $s^{-1}$). In general, we decreased the PAR values at 250 µmol PAR $m^{-2}$ $s^{-1}$ intervals. However, specific comparison between shade and sun leaves required more detailed measurements, from 100 to 0 µmol PAR $m^{-2}$ $s^{-1}$. In this case, PAR values were decreased at 10 µmol PAR $m^{-2}$ $s^{-1}$ intervals. All the Pn-light curves were performed at constant $CO_2$ concentration (400 mol $mol^{-1}$). Air and leaf temperature were measured with a thermocouple located inside the cuvette of the fluorometer. Leaf temperature was maintained constant for all the Pn-light curves (28°C). Relative humidity inside the cuvette was about 60%. Measurements were performed between 8 and 11 solar times.

Leaf photosynthesis was estimated from Pn-light curves data, for the 60 leaves tagged within the canopy. Then, dPn was calculated by integrating hourly data. dPn was determined for trees with different SWP values. Relationships between dPn and dIPAR were adjusted to the model that obtained the best fit. The statistical significance of the adjusted models was established for $p<0.001$. Sigma plot was used for these analyses.

## RESULTS

During Stage III, FI trees received 230 mm of water and NI trees no irrigation. Accumulated rain was 3 mm and FI maintained mid-day SWP values around -0.65 MPa (Fig. 1). NI caused significant reduction in SWP compared to FI trees. In NI trees, SWP values of -2.1 MPa were observed at harvest (Fig. 1).

Daily patterns of leaf incident PAR varied from leaf-to-leaf, but some general patterns were observed (Fig. 2). Leaves located in the top of the scaffolds, with an east orientation, intercepted high values of PAR early in the morning and low values in the afternoon. The opposite behavior was observed for leaves located at the top of the scaffold, with a west orientation. Leaves located at medium height within the canopy had a similar behavior to leaves located at the top of the canopy, but in general, the values of incident PAR were lower. Leaves located at the bottom of the canopy intercepted low values of PAR during the whole day.

Photosynthetic properties of sun and shade leaves were different (Fig. 3). Under non-water stress conditions (SWP about -0.65 MPa), shade leaves had lower light compensation points than sun leaves. Saturation of photosynthetic $CO_2$ assimilation rates, with light for shade and sun leaves, was about 7 and 1250 µmol $m^{-2}$ $s^{-1}$, respectively (Fig. 3). These values were reduced with NI. Water stress did not reduce photosynthetic $CO_2$ assimilation rates at low PAR values (<125 µmol $m^{-2}$ $s^{-1}$) (Fig. 3).

dIPAR varied from leaf-to-leaf (Fig. 4). For a given scaffold, the highest dIPAR values were observed at the top of the tree (about 40 mol $m^{-2}$ $day^{-1}$). dIPAR was reduced for leaves located at medium height within the canopy and very low values were observed for leaves located at the bottom of the tree (< 5 mol $m^{-2}$ $day^{-1}$). The relationship between dIPAR and dPn had a y-intercept of approximately zero, regardless of tree water status (Fig. 5). However, NI reduced dPn at high dIPAR values (Fig. 5).

## DISCUSSION

In this study, we evaluated relationships between daily photosynthesis (dPn) and daily leaf light interception (dIPAR), of ‘Ryan’s Sun’ peach subjected to full irrigation (FI), and no irrigation (NI), for 50 days before harvest. The values of SWP observed in FI were indicative of no water stress (Fig. 1). Under these circumstances there was a significant positive relationship between dIPAR and dPn (Fig. 5). The relationship had a zero y-intercept, the slope was similar to the linear relationship reported for ‘Fantasia’ nectarine by Rosati et al. (2002), and almost no saturation of dPn was observed at high dIPAR values. Our results suggest that all leaves of the canopy had similar photosynthetic radiation use efficiency (PnRUE) under FI. Considering constant PnRUE, it could be useful to estimate canopy photosynthesis from leaf photosynthetic properties, and the amount of light intercepted by the tree.

Constant PnRUE within the canopy was clearly not observed under water stress conditions (Fig. 5). When the values of SWP, achieved in NI, were indicative of moderate water stress (SWP between -1.2 and -1.5 MPa), leaves with dIPAR values higher than 20 mol $m^{-2}$ $day^{-1}$ had a significant reduction in dPn (Fig. 5). When the values of SWP achieved in NI were indicative of severe water stress (SWP between -1.7 and -2.2 MPa), leaves with dIPAR values higher than 5 mol $m^{-2}$ $day^{-1}$ had a significant reduction in dPn (Fig. 5). Only shade leaves were able to maintain their photosynthetic capacity under severe water stress.

The simple approach for modelling canopy photosynthesis from leaf photosynthetic properties and the amount of light intercepted by the tree would clearly not be valid under water stress conditions where additional information of leaf light interception within the canopy would be necessary. This could be obtained with functional structural models such as L-Peach-d (Allen et al., 2005; Lopez et al., 2008b, 2010). Incorporation of functions, such as those observed in Figure 5, into L-Peach-d may produce realistic simulations of whole-canopy photosynthesis, under water stress. The results presented in this study may be also useful to validate other models that are able to simulate individual leaf light interception, water potential, and photosynthesis, under different irrigation conditions (L-Peach-h) (Da Silva et al., 2011).

## ACKNOWLEDGEMENTS

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## Figures

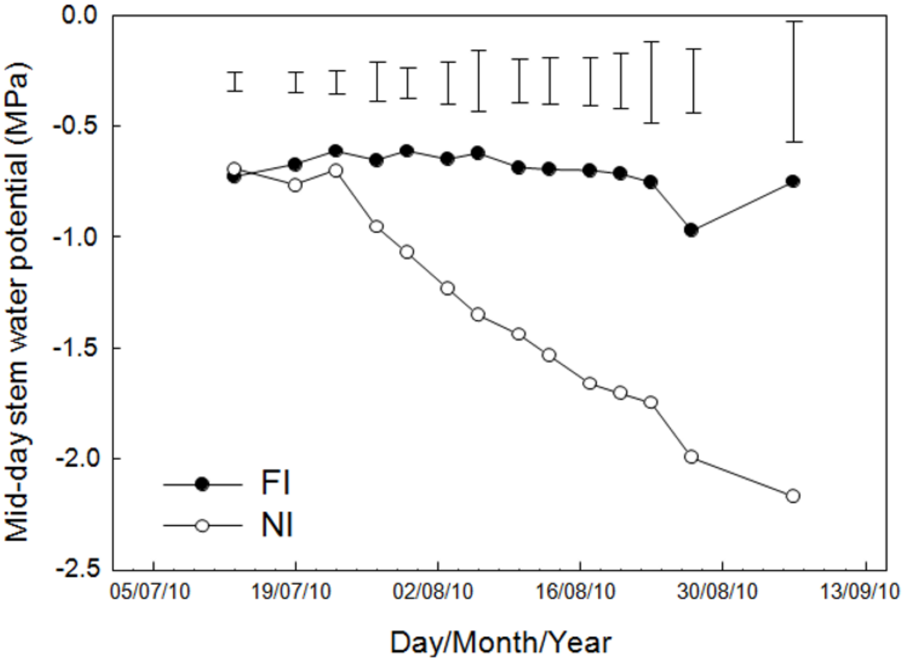

Fig. 1. Mid-day stem water potential during Stage III for trees under full irrigation (FI) and no irrigation (NI). Bars represent the least significant difference for the treatments.

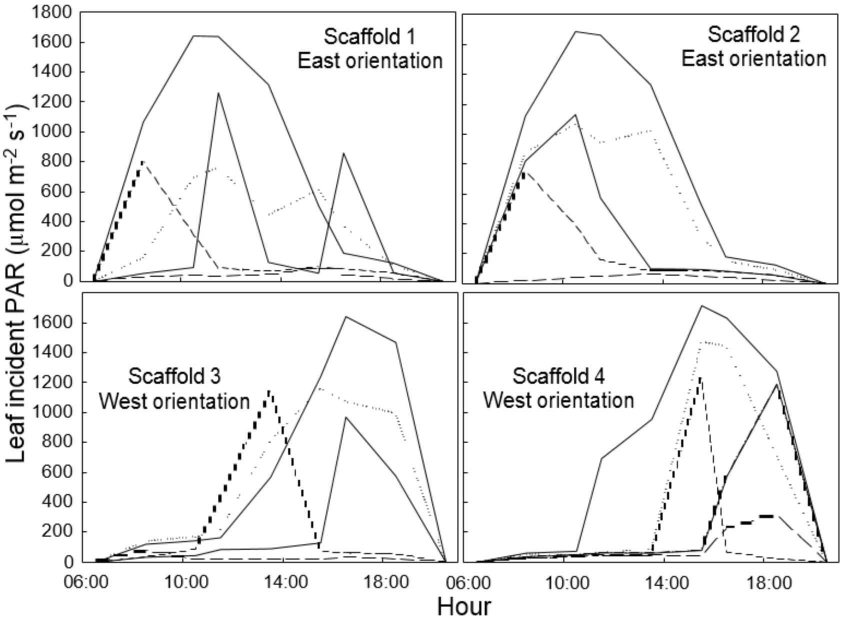

Fig. 2. Diurnal patterns of leaf incident photosynthetically active radiation (PAR) for selected leaves within the canopy. Each line represents one leaf.

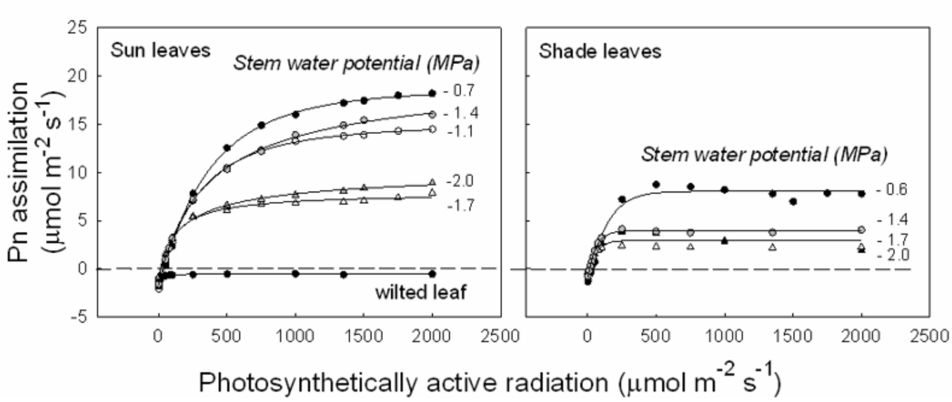

Fig. 3. Photosynthetic light response curves, in sun and shade leaves, for different mid-day stem water potential (SWP) values, during Stage III. Each point represents the mean value of 3 curves.

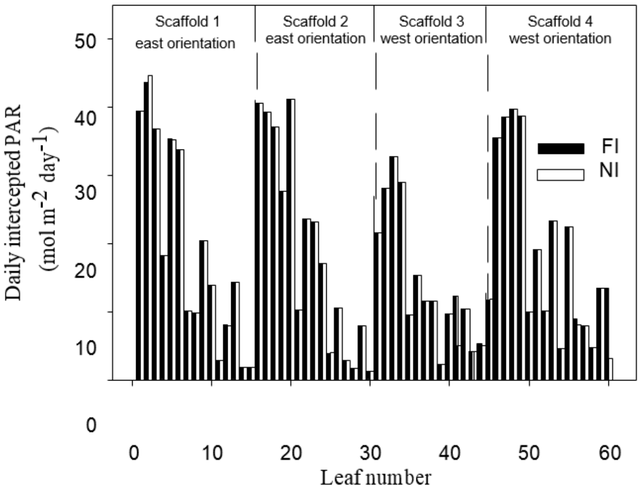

Fig. 4. Daily leaf intercepted photosynthetically active radiation (dIPAR) for 60 leaves, for FI and NI trees. Each bar represents a leaf, and dIPAR was calculated by integrating hourly leaf intercepted PAR data. Each leaf was assigned with a number (x axis), and it represents the order for the hourly leaf intercepted PAR measurements. For each hourly measurement, we always started with the scaffolds oriented to the east (scaffold 1 and 2), and then, to those oriented to the west (scaffolds 3 and 4). For a given scaffold, we always started from the top of the tree. Fifteen leaves were measured for each scaffold.

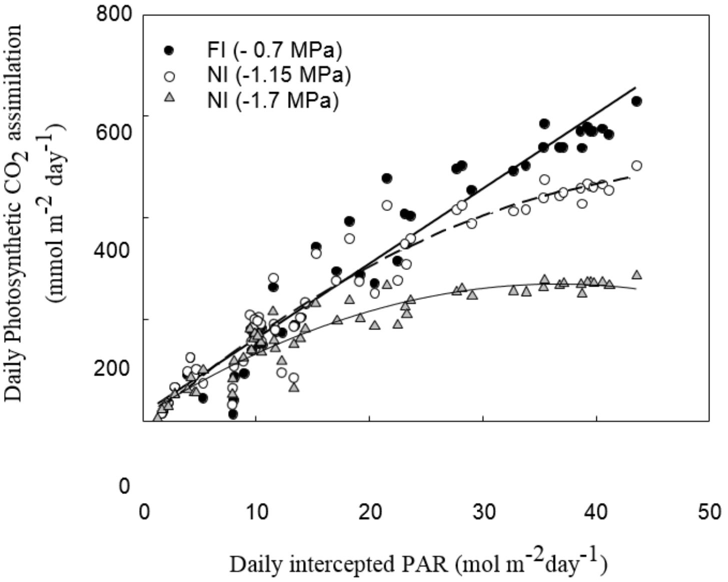

Fig. 5. Relationship between daily leaf intercepted PAR (dIPAR) and daily leaf photosynthesis (dPn), for different levels of mid-day stem water potential (SWP). Relationships were adjusted to a simple linear regression model under full irrigation (FI), and to polynomial (second degree) regression models under no irrigation (NI). Each point represents a leaf.