Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat

Physiological responses of apricot and peach cultivars under progressive water shortage: Different crop signals for anisohydric and isohydric behaviours

Pasquale Losciale [a,*], Liliana Gaeta [b], Mariadomenica Corsi [a], Ciro Galeone [c], Luigi Tarricone [d], Rita Leogrande [b], Anna Maria Stellacci [a]

[a] Department of Soil, Plant and Food Sciences, University of Bari "Aldo Moro", 70126 Bari, Italy
[b] Council for Agricultural Research and Economics, Research Centre for Agriculture and Environment, 70125 Bari, Italy
[c] Department of Biology, University of Bari "Aldo Moro", 70126 Bari, Italy
[d] Council for Agricultural Research and Economics, Research Centre for Viticulture and Enology, 70010 Turi, Italy

A B S T R A C T

The knowledge about the behaviour of different fruit tree species when subjected to water shortage is pivotal to pair correctly the species with the environment, as well as to choose the most reliable index for monitoring the plant water status. Net photosynthesis (Pn) and stomatal conductance (gs) are considered some of the most reliable variables describing the plant water status, functionality and potential productivity, but their measurement are actually time consuming, complex and expensive. The aims of the present study were to investigate the effect of a progressive water stress on leaf functioning and plant water status of two stone fruit trees species; to study the water relations within the Soil-Plant-Atmosphere Continuum; to assess a pool of indices for estimating Pn and gs by means of other variables quick to be measured, potentially through less expensive and user-friendly sensors. The trial was carried out on an early ripening apricot variety (*Prunus armeniaca* L. cv. Primius) and on a late ripening peach variety (*Prunus persica* (L.) Batsch cv. Calred) subjected to progressive dry down. Trees were monitored for stem water potential, leaf temperature, chlorophyl fluorescence, Pn and gs. "Primius" and "Calred" behaved as near anisohydric and near-isohydric plants, respectively. In "Primius" Pn and gs were more affected by soil water content than vapour pressure deficit (VPD) and the opposite occurred in "Calred", suggesting a different approach to be used for managing water in the two cultivars. Chlorophyll fluorescence variables and leaf to air temperature difference (ΔT), combined properly by means of stepwise multiple regression analysis approach, were selected as good predictors of Pn for both the species. ΔT and VPD were selected to estimate gs, using the same approach. The prediction performance of the models resulted good suggesting their possible use for driving irrigation in a more sustainable and plant-based way.

1. Introduction

Water controls vital functions as photosynthesis (through stomata opening), thermoregulation, and transport of different compound among the plant organs. Monitoring plant water status allows farmers and technicians to sustain the yields and the quality of the product (Fernández, 2014; Levidow et al., 2014), especially in the warmer seasons (Stöckle et al., 2011; Snyder, 2017). Managing water supply is crucial for fruit tree as production and quality are strictly related to an appropriate tree water status. The starting investment to realize the

orchard is very high and, as perennial, fruit tree can bear the consequences of water stress occurring in one season even in the next one (Manfrini et al., 2018). Trees affected by water stress, show a reduction in the rate of CO_2 assimilation, above all during the hottest hours of the day (Chaves, 1991). This decrease has been attributed to the partial stomata closure in the hottest hours of summers days, resulting from imbalance between the high water demand of the air and the low water supply due to the low soil moisture. In addition, the decrease of the transpiration rate reduces the cooling effect, increasing the leaf temperature. As a consequence, photoinhibition, the recovery from

photodamage and, above all, photorespiration (whose activity increases with leaf temperature) could lead to an additional loss of carbon fixed (Foyer and Harbinson, 1994; Losciale et al., 2011a; Murata and Nishiyama, 2018; Yi et al., 2022). The scientific community is already at work to answer to this request by developing a variety of methods and technologies aiming at reducing water supply and water losses and at scheduling irrigation in an efficient way. Nowadays, the agronomists have to rely on information from several sources (soil, plant and atmosphere) to properly manage the irrigation requirements of the crops. However, it is necessary to keep in mind the characteristics related to the types of data acquired. Microclimate variables can be representative of a large area and can be easily measured by few stations for a vast land extension. However they may not be nearby a given farm, thus the local microclimate is not taken into account (Allen et al., 1998; Jones, 2004). Soil water content monitoring is usually used for irrigation scheduling (Cardenas-Lailhacar and Dukes, 2010; Soulis et al., 2015); but, where the soil is very heterogenous, a large number of sensors is necessary to cover its variability and to have a good representativeness of the measure (Jones, 2004). The plant-based indices and the related sensors, which directly measure the plant water status, are not often taken into consideration because of several constrains: time-consuming, expensiveness of the instruments, difficulty of results interpretation, a not fully mature technology (Fernández, 2017). In fact, some among the plant-based sensors are widely used mainly in scientific area due to the instrument complexity but also their costs. In addition, it is important to choose the plant-based index and sensor according to the specie to monitor. For example, the stem water potential is a very informative index (Naor, 2006), however it is necessary to carefully interpret the data above all when an isohydric species is monitored. Isohydric plants tend to maintain a stable water potential closing stomata and reducing stomatal conductance and net photosynthesis (Turner et al., 1985; Socías et al., 1997). As a consequence, this behaviour masks the real reduction of carbon fixation as a slight decrease of stem water potential is observed. Apricot (*Prunus armeniaca* L.) and Peach (*Prunus persica* (L.) Batsch), for example, are considered stone fruit species having a contrasting behaviour in regulating their water relations. Apricots was considered able to maintain stomata opened by osmotic adjustment even when water potential is low (Loveys et al., 1987). However, its drought avoidance behaviour linked to stomatal closure was also observed in other experiments (Torrecillas et al., 1999; Ruiz-Sánchez et al., 2007). Also peach, considered an-isohydric in some studies (Xiloyannis et al., 1980), showed a good stomatal regulation preventing the decay of water potential in other experiments (Steinberg et al., 1989; Losciale et al., 2020). As for other species, like Grapevine, also in these cases the strategies for regulating the water relations could be cultivar and specie dependent (Shultz, 2003). Nevertheless, plant-based measurements are widely considered the most reliable indicators to assess water status and to schedule irrigation (Lakso et al., 2022). The reason is that plant-based measurement (and the related sensors) relies on using the plant as a biosensor, which integrates the soil and atmosphere water status as well as the plant physiological response to available water (Fernández, 2017; Levin and Nackley, 2021). Several research groups reported that some of the most informative variables on the plant water status would be the net photosynthesis rate and stomatal conductance (Flexas and Medrano, 2002; Jones, 2004; Cifre et al., 2005; Hernandez-Santanaa et al., 2019; Zhang et al., 2021) as they are strictly related to plant water status and consumption as well as to potential productivity. However, the direct measure of net photosynthesis by means of Infra-Red Gas Analysers (IRGAs) is time consuming and needs very expensive instruments and skilled personnel.

The aims of the present study were: (i) to elucidate the effect of a progressive water stress on leaf functioning and plant water status of two different stone fruit trees species: Apricot (*Prunus armeniaca* L.) and Peach (*Prunus persica* (L.) Batsch); (ii) to set-up one or more indices able to estimate the leaf functioning on plant species potentially having different strategies to cope with the water shortage. The indices should be reliable, fast to be measured and potentially exploitable in new generation Decision Support Systems for Smart Agriculture.

2. Materials and methods

The trial was carried out in the summer 2019 at the Research Centre for Agriculture and Environment of the Council for Agricultural Research and Economics, Bari (CREA-AA, Bari) on 3 years old peach (*Prunus persica* (L.) Batsch) cv. "Calred" and apricot (*Prunus armeniaca* L.) cv. "Primius", grafted on "GF677″ and "Tetra" rootstocks, respectively. In addition to belong to different species, the two cultivars under investigation were also divergent for the fruit ripening period and for the time of presence of fruit attached to the tree: "Primius" is an early ripening cultivar with a short time range between flowering and ripening, vice versa for "Calred". Trees were planted in pots (30 litres of volume) with the same amount and type of soil. Soil texture was classified as clay loam, with a dry bulk density of 1.15 t m^{-3} and soil water content in volume at field capacity (FC, −0.03 MPa) and wilting point (WP, −1.5 MPa) were 0.34 and 0.19 m^{3}m^{-3}, respectively. In order to have an uniform canopy, trees were pruned back every year maintaining about 8–10 shoots per tree without fruits. Plants were managed according to the regular practices and irrigation was provided daily restoring the field capacity. Ten plants per species were selected for the trial. On July 24th (205 Day Of the Year, DOY) all the potted plants were irrigated to field capacity allowing the drainage of the free water. In order to reduce the soil evaporation, the soil of each pot was covered with a plastic film in turn covered with aluminium foil to avoid any increase of soil temperature due to light absorption. A half of them continued to be irrigated daily till the field capacity, while the remaining trees were left without irrigation in order to allow their dehydration. Starting from 205 DOY, from 11.00 to 14.00, the following measures were taken on each plant: soil water content, (SWC, m^{3}m^{-3}), expressed as volume of water per volume of soil, stem water potential (Ψs, MPa), with a Scholander pressure chamber according to the protocol proposed by Naor et al. (1995); leaf net photosynthesis (Pn, μmol m^{-2} s^{-1}); stomatal conductance (gs, mol m^{-2} s^{-1}); transpiration (Tr, mmol m^{-2} s^{-1}); electron transport rate exiting from the PSII (J$_{PSII}$, μmol m^{-2} s^{-1}), (Genty et al., 1989; Maxwell and Johnson, 2000); electron transport rate exiting PSII and used for net carboxylation (J$_{CO2}$, μmol m^{-2} s^{-1}) and for non-net carboxylative processes (J$_{NC}$, μmol m^{-2} s^{-1}) such as photorespiration, alternative transports and dark respiration (Losciale et al., 2010; Losciale et al., 2011b); P$_{KO/KC}$ (Losciale et al., 2015); leaf and air temperature and its difference (T$_{leaf}$, T$_{air}$, ΔT, °C); air vapour pressure deficit (VPD, kPa). P$_{KO/KC}$ was calculated as J$_{PSII}$* (KO/KC) where KO and KC are the Michaelis-Menten constants for photorespiration and carboxylation, respectively (Bernacchi et al., 2001; Diaz-Espejo, 2013). This variable takes in account both the amount of electron exiting from PSII and the carboxylative/photorespiratory activity of RuBisCO (Losciale et al., 2015). Pn, gs, Tr, VPD, J$_{PSII}$, J$_{NC}$, P$_{KO/KC}$, T$_{leaf}$ and T$_{air}$, were measured, using an open circuit infrared gas exchange system fitted with a leaf fluorimeter and a LED light source (Li-Cor 6400XT, LI-COR inc., Lincoln Nebraska U.S.A.). The actinic light was set at 1200 μmol m^{-2}s^{-1}, allowing the light saturation of photosynthesis without any unrecoverable photo-damage. The contemporary measures performed on the daily irrigated trees allow us to check the presence of some variation of leaf functionality not linked to water limitations.

This routine was repeated for 3 consecutive cycles of dehydration: Cycle I, from 205 to 207 DOY, with 2 days of dehydration; Cycle II, from 211 to 214 DOY with 3 days of dehydration; Cycle III, from 238 to 248 with 10 days of dehydration.

2.1. Preliminary statistical analysis

Descriptive statistics were first computed to synthesize the main features of data distribution. Indices of central tendency and position (mean, median), dispersion (sum of squares, variance, standard

deviation) and shape (skewness and kurtosis) were computed for the variables selected as response variables describing plant water status and functionality (leaf net photosynthesis and stomatal conductance). In addition, normality test of Kolmogorov-Smirnov was applied in order to verify the assumption of Gaussian distribution.

2.2. Leaf functionality and water relations within the Soil-Plant-Atmosphere Continuum

The relation between stomata closure (gs) and J_{PSII}, J_{CO2}, J_{NC}, as well as the relation between stem water potential (Ψs) vs. Pn and gs were analysed for both the species. A correlation analysis was also performed between Pn and gs with SWC (expressing the water availability in the soil) and with VPD, representing the water demand of the environment.

2.3. Stepwise linear regression analysis

In order to investigate the relationships between net photosynthesis, stomata conductance and predictor variables and to select the predictors most influencing their estimation, linear regression models were fitted, and the stepwise selection algorithm was used. The methods were applied considering leaf net photosynthesis (Pn) and stomatal conductance (gs) as dependent variables and as predictors: the soil water content, VPD, T_{leaf}, T_{air}, ΔT, Fm', Fs, J_{PSII}, $P_{KO/KC}$. The significant level to entry and to stay was set to 0.05. The variables chosen as candidate predictors for net photosynthesis and stomatal conductance had to have the following peculiarities: fast measurement, possibility to be detected by a future cost affordable sensor, physiological meaning. Stem water potential variable was not considered as an appropriate predictor in the stepwise analysis since its detection by means of a pressure chamber did not match the peculiarities reported below. Studies on the development and calibration of instruments for measuring the stem water potential continuously and at low cost are in progress (Lakso et al., 2022; Pagay, 2022), but in the present research it was not possible to test them.

Models developed for each crop and for both the variables were trained on the 75% of the dataset randomly collected for each species. Afterwards validation was performed on the remaining 25% of the dataset not used for training the model, comparing the estimated values of Pn and gs with their direct (observed) measures. The prediction performance of the models developed was tested by means of the Residual Prediction Deviation (RPD), calculated as the ratio between the standard deviation of the observed variables and the root mean square error for the training and for validation, respectively. According to Chang et al. (2001) and Bellon-Maurel et al. (2010), RPD higher than 2.0 indicated an excellent prediction performance; with values between 1.4 and 2.0 models were considered fair models and below 1.4 they were classified unreliable. Descriptive statistic and regression analyses were performed with STATISTICA 7.0 software.

3. Results

The three cycles of measurements were characterized by different weather conditions (Table 1). During the time of measure, the highest values of air temperature (T_{air}) and VPD were recorded in the second cycle, whereas in the third cycle T_{air} and VPD reached their lowest values (Table 1).

At the beginning of each cycle all the trees were irrigated till the field capacity and half of them were allowed to lose water via transpiration not adding water. During the first two cycles, after two days of dehydration, the soil water content was 0.25 $m^3 m^{-3}$ in both the species, reducing the available water by about 60%; during the cycle II, after three days of dehydration, the available water was further reduced by 20% and 27% for apricot and peach, respectively. The third dehydration cycle was longer than the previous ones, lasting 10 days. At the end of cycle III, SWC was 0.23 and 0.22 $m^3 m^{-3}$ for apricot and peach respectively.

3.1. Descriptive statistic

The data recorded along the experiment for each species (128 records for each one) showed a range of variation for Pn and gs of 20.06 $\mu mol\ m^{-2} s^{-1}$ and 0.215 $mol\ m^{-2} s^{-1}$ for apricot and of 27.24 $\mu mol\ m^{-2} s^{-1}$ and 0.37 $mol\ m^{-2} s^{-1}$ for peach (Table 2). Pn and gs for both species were normally distributed or with slight deviation from the normal distribution, as indicated by the normality test results and by the analysis of the skewness and kurtosis coefficients, which were close to zero (Table 2).

3.2. Water relations and leaf functionality in the two species

Stomatal conductance (gs) and net photosynthesis (Pn) were linearly related in the two species as well as the electron transport rate exiting PSII (J_{PSII}) and gs (Fig. 1). The homogeneity of the slopes test showed no differences between the two species when gs was related to Pn, J_{CO2} (F=0.0059, p = 0.94), J_{PSII} (F=0.0043, p = 0.95) and J_{NC} (0.0014, p = 0.97). The relation between stomatal conductance and J_{PSII} appeared more scattered and the reduction of J_{PSII} with gs was less pronounced than the decrease of net photosynthesis expressed as the electron flux density fixed as organic CO_2 (J_{CO2}). The electron transport rate exiting PSII and funnelled to non-net carboxylative transports (J_{NC}) remained quite stable not changing with gs variation (Fig. 1C, D).

The variation of net photosynthesis and stomatal conductance as a function of stem water potential was different between the two species. In "Primius" apricot Pn and gs remained quite stable while the stem water potential (Ψs) decreased with the progressive water shortage. Net photosynthesis and stomata conductance slightly decreased with Ψs when it reached values lower than -1.5 MPa (Fig. 2A,C). In "Calred" cultivar, with values of stem water potential around -1.0 MPa, gs and Pn varied from ~ 0.27–0.08 $mol\ m^{-2} s^{-1}$, for gs; and from ~ 22–5 $\mu mol\ m^{-2} s^{-1}$, for Pn. Afterwards net photosynthesis and stomata conductance did not further decrease while Ψs showed a reduction till values around -2.7 MPa (Fig. 2B,D).

Stomatal conductance and net photosynthesis appeared more related to soil water content ($R^2 = 0.69$ and 0.70, respectively) than to air Vapour Pressure Deficit ($R^2 = 0.03$ and 0.07, respectively), in apricot (Fig. 3). In "Calred" peach, gs and Pn were more related with VPD ($R^2 = 0.46$ and 0.49, respectively) than with SWC, showing R^2 of 0.34 and 0.31, respectively (Fig. 4). The species caused a significant difference in the relationship VPD vs. Pn (F=9.09, p = 0.003) and VPD vs. gs (F=13.91, p < 0.01).

3.3. Stepwise regression analysis

3.3.1. Net photosynthesis estimation

The stepwise regression analysis selected $P_{KO/KC}$, ΔT and VPD for Pn estimation in both the species. The Adjusted R^2 (Adj. R^2) increased progressively with the inclusion of the variables (Table 3). Adj. R^2 reached 0.7 when $P_{KO/KC}$ and ΔT were added and it increased to 0.75 and 0.78 for apricot and peach, respectively, when VPD was also included (Table 3). Considering the relatively small increase of Adj. R^2 recorded with the inclusion of VPD and, according to the aim of the

Table 1

Average, maximum and minimum values of air temperature and VPD recorded during the three dehydration cycles (Cycle I: 205–207 DOY; Cycle II: 211–214 DOY; Cycle III: 238–248).

Cycle	VPD (kPa)			T_{air} (°C)		
	av	min	max	av	min	max
I	3.11	2.59	3.90	34.91	31.07	37.17
II	3.69	2.95	4.29	36.05	32.39	37.40
III	2.59	1.88	3.04	33.22	29.06	34.78

Table 2

Descriptive statistics and normality tests for net photosynthesis and stomatal conductance values collected on Apricot cv. Primus and Peach cv. Calred.

| Specie	Variable	min	max	mean	median	skewness	Kurtosis	Kolmogorov-Smirnov D (p)
Apricot	Pn (μmol m^{-2}s^{-1})	1.55	21.61	13.66	14.10	-0.57	0.15	0.10 (<0.2)
	gs (mol m^{-2}s^{-1})	0.015	0.230	0.129	0.132	-0.24	-0.43	0.05 (>0.2)
Peach	Pn (μmol m^{-2}s^{-1})	0.56	27.80	12.72	12.55	0.32	-0.49	0.63 (>0.2)
	gs (mol m^{-2}s^{-1})	0.014	0.383	0.138	0.119	0.79	-011	0.12 (<0.1)
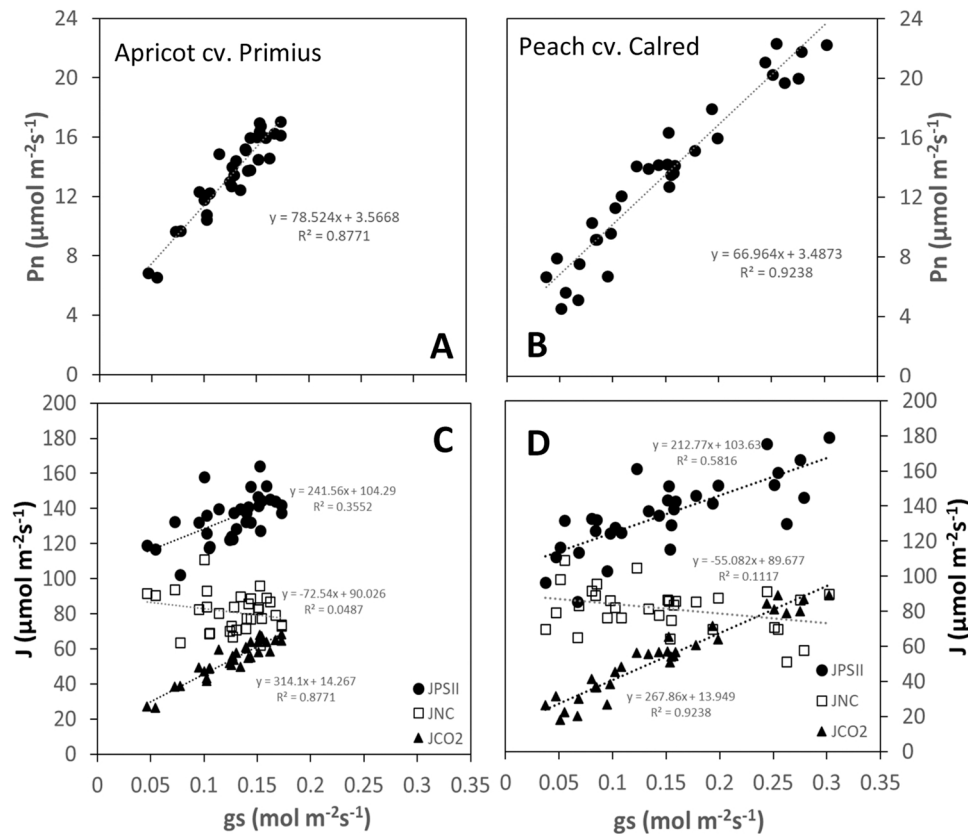
Fig. 1. Relationship between stomatal conductance, gs, and net photosynthesis, Pn (A,B), and (C,D) between gs and the electron transport rate exiting PSII (J_{PSII}) and funneled to net photosynthesis (J_{CO2}) or to non-net carboxylative transports (J_{NC}) in apricot cv. "Primius" (A,C) and peach cv. "Calred" (B,D), subjected to 3 dehydration routines. Each point is the average of 5 measures.

present study, the prediction performance of the models assessed taking in account $P_{KO/KC}$, ΔT or adding also VPD were evaluated. When the three variables were considered as predictors, $F_{(3,92)}$ values were 98.73 and 116.49 for apricot and peach, respectively, with a P-value < 0.00001 for both the species. The standard error of estimate was 1.93 and 2.90 μmol m^{-2}s^{-1} for "Primius" and "Calred" cultivars, respectively. The Durbin-Watson (DW) index (1.99 for apricot and 1.92 for peach), together with the distribution of the residuals, revealed the absence of serial autocorrelation and the homoscedasticity of the residuals. Considering $P_{KO/KC}$ and ΔT as predictors $F_{(2,93)}$ was 108.65 and 13.48 for apricot and peach, respectively, and the P-value remained < 0.0001. The standard error of estimate was 2.16 and 3.4 mol m^{-2}s^{-1} for "Primius" and "Calred", respectively. The distribution of the residuals was homoscedastic and DW was around 2.0 (1.96 and 1.90 for apricot and peach, respectively), indicating the absence of serial autocorrelation. The Residual Prediction Deviation (RPD), used to evaluate the prediction performance of the models, showed values of 2.06 for apricot and 2.2 for peach, when the three variables were included in the model. RPD was 1.84 and 1.86 for apricot and peach when VPD was removed (Table 3). Validation, performed on the remaining 25% of dataset, showed a Residual Prediction Deviation of 1.84 for apricot and 1.56 for peach when $P_{KO/KC}$, ΔT and VPD were used as predictors. RPD

was 1.62 and 1.69 for "Primius" and "Calred", respectively, considering $P_{KO/KC}$ and ΔT as independent variables for the models (Table 3). The resulting relation between the observed and the estimated net photosynthesis was linear with a 1–1 relation for both the species and taking into account all the three variables or $P_{KO/KC}$ and ΔT (Figs. 5,6).

3.3.2. Stomatal conductance estimation

The stepwise analysis selected ΔT, VPD, $P_{KO/KC}$ and ΔT, VPD, considering apricot and peach dataset respectively. The Adjusted R^2 reached values of 0.81 in apricot and 0.78 in peach when ΔT and VPD were considered. In apricot it further increased at 0.84 including also $P_{KO/KC}$ as predictor. As mentioned for Pn estimation, considering the relatively small increase of Adj. R^2 with $P_{KO/KC}$ inclusion and, since this variable was excluded in the stepwise for peach, the linear regression models for gs estimation were finally performed using ΔT and VPD to refine the estimation parameters during the training step. Values of $F_{(2,93)}$ recorded for apricot and peach were 209.88 and 153.15, respectively, with a p-value < 0.00001. The standard errors for estimate were 0.019 and 0.04 mol m^{-2}s^{-1} for "Primius" and "Calred", respectively. The Durbin-Watson index values, around 2.0 (1.96 and 2.10 for apricot and preach, respectively) revealed the absence of serial autocorrelation; homoscedastic distribution of the residuals was observed for both the
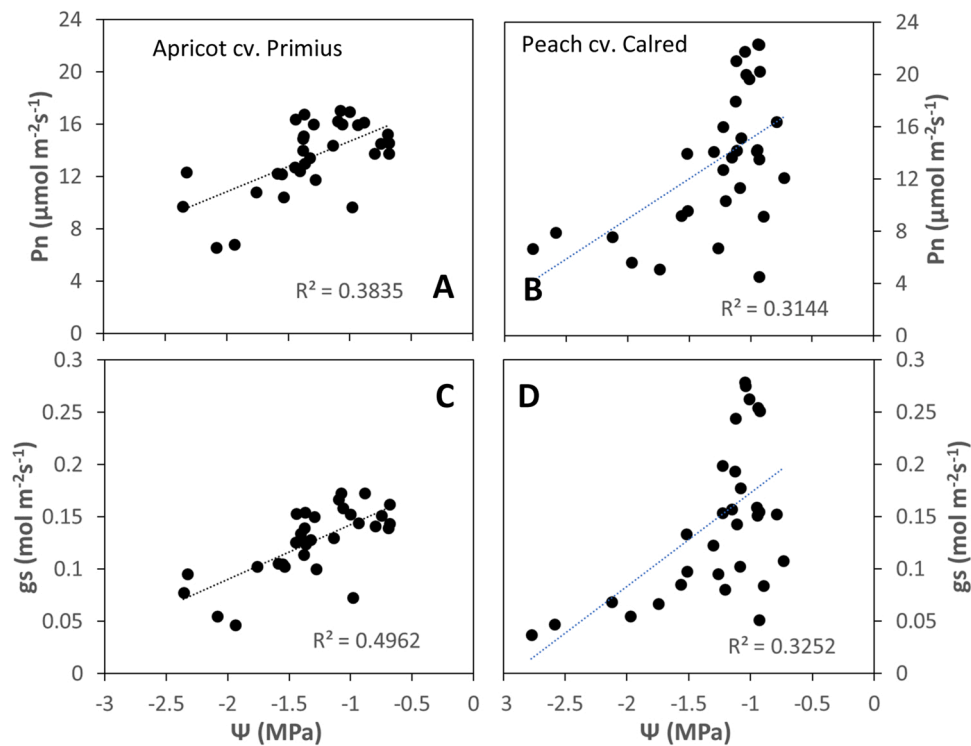
Fig. 2. Relationship between stem water potential (Ψs) and net photosynthesis, Pn (A,B), and between Ψs and stomatal conductance, gs (C,D) in apricot cv. "Primius" (A,C) and peach cv. "Calred" (B,D), subjected to 3 dehydration routines. Each point is the average of 5 measures.

species (Fig. 7). The Residual Prediction Deviation calculated on 75% of dataset used for training the models showed values of 2.36 and 2.08 for apricot and peach, respectively. RPD was 2.36 and 1.77 for "Primius" and "Calred" cultivars, when the 25% of the remaining dataset was used for validating the obtained models (Table 4). The relation between the observed and the estimated values of stomatal conductance was linear with a 1–1 relation for both the species (Fig. 7).

4. Discussion

4.1. Water relations and leaf functionality in the two species

Stomatal conductance (gs) and net photosynthesis (Pn) were linearly related and with the same slope in "Primius" and "Calred", suggesting the high influence of stomatal activity on leaf carboxylation and a similar behaviour of both the species (Fig. 1A,B). The intrinsic Water Use Efficiency (IWUE) calculated as the ratio between Pn and gs (the slope of the line) remained quite constant, indicating that water productivity due to stomatal conductance did not change with the increase of gs and that the stomatal threshold to reach the maximum photosynthesis was not reached yet. A similar behaviour was also observed in apple cv. Fuji but when it was covered with a blue shading net IWUE decreased with the increase of gs (Bastías et al., 2021). This last pattern is in accordance with several studies where a curvilinear relation between Pn and gs was observed (Cheng et al., 1996; Torrecillas et al., 1999; Flexas et al., 2002; Cifre et al., 2005). In this case water productivity due to stomatal conductance decreased with the increase of gs indicating an extra water consumption for the same amount of CO_2 fixed.

The quenching partitioning analysis (Fig. 1C,D) showed how the reduction in stomatal opening limited the electron transport rate fixed by net photosynthesis (J_{CO2}) as well as the overall electron transport rate exiting PSII (J_{PSII}). However the relation between J_{PSII} and gs appeared more scattered and the rate of reduction of J_{PSII} was lower than that of J_{CO2} (Fig. 1C,D). This reduction was attenuated by the increased activity of non-net carboxylative transports like photorespiration, alternative

electron transports and dark respiration (J_{NC}). Despite the reduction of J_{PSII}, the electron transport rate exiting from PSII and funnelled to non-net carboxylative transports (J_{NC}) remained quite stable (Fig. 1C,D) and it assumed a greater importance while the electron sink of carboxylation was reduced with stomatal closure. Photorespiration and alternative electron transports acted as photoprotective mechanisms dissipating the excessive energy no more used for carbon fixation. This behaviour seemed to be quite common in C3 plants (Seaton and Walker, 1990; Osmond and Grace, 1995; Cifre et al., 2005) and it was observed in other fruit tree species subjected to progressive water shortages like grapevine, apple, pear and peach (Flexas et al., 2002; Losciale et al., 2008, 2011b, 2014).

"Calred" peach cultivar behaved as a near isohydric plant as the stem water potential (Ψs) remained quite stable while gs and Pn were reduced (Fig. 2B,D). The pessimistic (conservative) attitude of this late ripening cultivar was hypothesized in a previous field study where the effect of different soil water contents was compared on plant functionality and productivity (Losciale et al., 2020). Stomatal closure, reducing the connection with air, concurred to maintain stem water potential at a safety threshold against the risk of cavitation (Tardieu and Simonneau, 1998; Lauri et al., 2016). Instead, a near anisohydric behaviour was observed in "Primius" apricot cultivar where stomatal closure was not so effective in maintaining a stable Ψs (Fig. 2A,C). Stomatal conductance and leaf photosynthesis were differently related to soil water content (the water source) and to the evapotranspirative demand of the air (VPD, the water sink). In "Calred" peach, gs and Pn seemed to be more related to VPD (Fig. 4B) than to soil water content (Fig. 4A), while the opposite was observed in "Primius" apricot (Fig. 3A,B). This knowledge could be useful to manage the orchard properly. The use of stem water potential measures to drive irrigation could be appropriate in "Primius" apricot but not in "Calred" peach where Ψs remained quite stable while Pn was strongly reduced. Furthermore, under moderate water stress conditions, "Calred" peach could benefit from VPD modulation. Under semi-arid conditions, where VPD values could be limiting, the use of moderate shading net (shading power of 30%) reduced the VPD of about
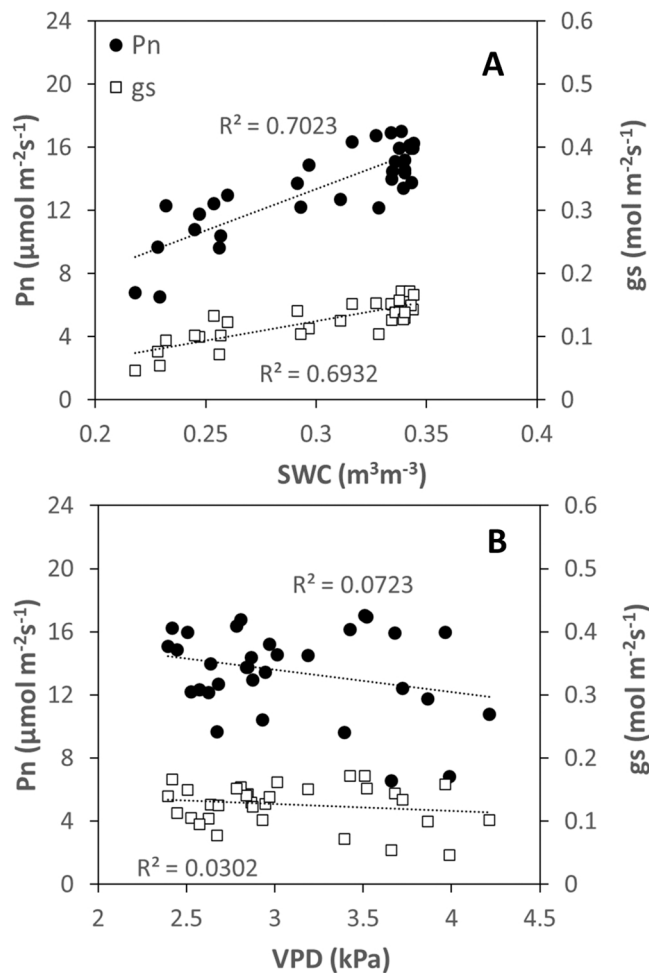
Fig. 3. Relationship between leaf functionality variables (Pn and gs) and the soil water content (A) and the Vapour Pressure Deficit (B), recorded in apricot cv. "Primius" during the three dehydration cycles. Each point is the average of 5 measures.

Fig. 4. Relationship between leaf functionality variables (Pn and gs) and the soil water content (A) and the Vapour Pressure Deficit (B), recorded in peach cv. "Calred" during the three dehydration cycles. Each point is the average of 5 measures.

15% (from an average of 3.4–2.9kPa during the summer period) favouring the fruit growth and yield (Campi et al., 2020). On the other hand, for "Primius" apricot it is very important to maintain a high soil water content to have a good carbon fixation.

4.2. Stepwise Multiple Regression Analysis

4.2.1. Net photosynthesis

The stepwise regression analysis selected the same 3 variables for both the species ($P_{KO/KC}$, ΔT and VPD) and the adjusted R^2 increased progressively while the variables were added into the model. In particular, when the first two variables ($P_{KO/KC}$ and ΔT) entered in the model the adjusted R^2 reached values of about 0.70 (Table 3). While in the training step the Residual Prediction Deviation (RPD) lowered from values > 2.0 to around 1.8 considering three or two variables, respectively, during the validation step (a more restrictive phase of model assessment) RPD remained within the range 1.4–2.0 using $P_{KO/KC}$ and ΔT or also adding VPD as predictors (Table 3). In both the cases, the models were considered fair models (Chang et al., 2001; Bellon-Maurel et al., 2010). The use of two variables instead of three did not affect very much the prediction performance of the models (Table 3). This was also confirmed by the resulting relationship between the observed and the estimated Pn, linear and with a 1–1 relation (Figs. 5B,6B). A similar stepwise approach selected the same variables to estimate net photosynthesis (I_{PL} index) in apple and pear (Losciale et al., 2015), suggesting
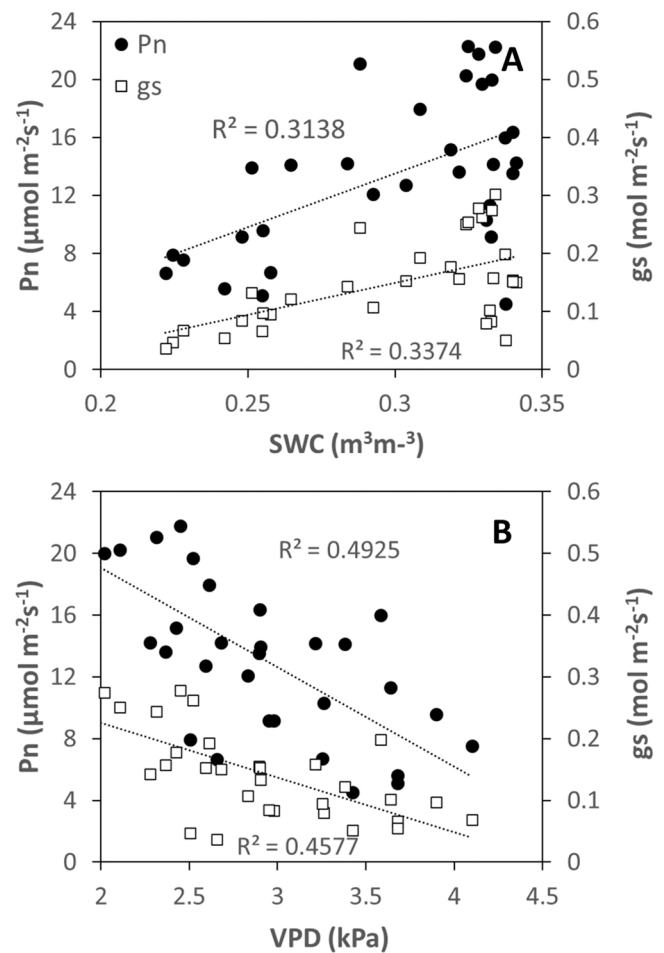
the high physiological meaning of these variables in describing leaf functionality and water status (Laurens et al., 2018; Coupel-Ledru et al., 2019; Yang et al., 2021). In pear, the use of estimated Pn as plant indicator to drive irrigation allowed to reduce water supply of about 50%

Table 3
Prediction performances of the models for Pn estimation, expressed as adjusted R^2 (Adj.R^2), Root Mean Square Error (RMSE) and Residual Prediction Deviation (RPD), obtained considering $P_{KO/KC}$, ΔT, VPD or $P_{KO/KC}$, ΔT, as predictors.

Step	Specie	Variable	Predictors ($P_{KO/KC}$, ΔT, VPD)	Predictors ($P_{KO/KC}$, ΔT)
Training	Apricot cv. "Primius"	Adj.R^2	0.75	
				0.70
		RMSE	1.89	
				2.13
		RPD	2.06	
				1.84
	Peach cv. "Calred"	Adj.R^2	0.78	0.70
		RMSE	2.83	3.34
		RPD	2.2	1.86
Validation	Apricot cv. "Primius"	RMSE	1.90	
				2.16
		RPD	1.83	
				1.62
	Peach cv. "Calred"	RMSE	4.07	3.79
		RPD	1.56	1.69

Fig. 5. Relation between observed Pn (Pn_obs) and estimated with $P_{KO/KC}$, ΔT and VPD as predictors (A) or removing VPD (B), in apricot cv. "Primius". The complete dataset has been reported in the graphs (n = 128).

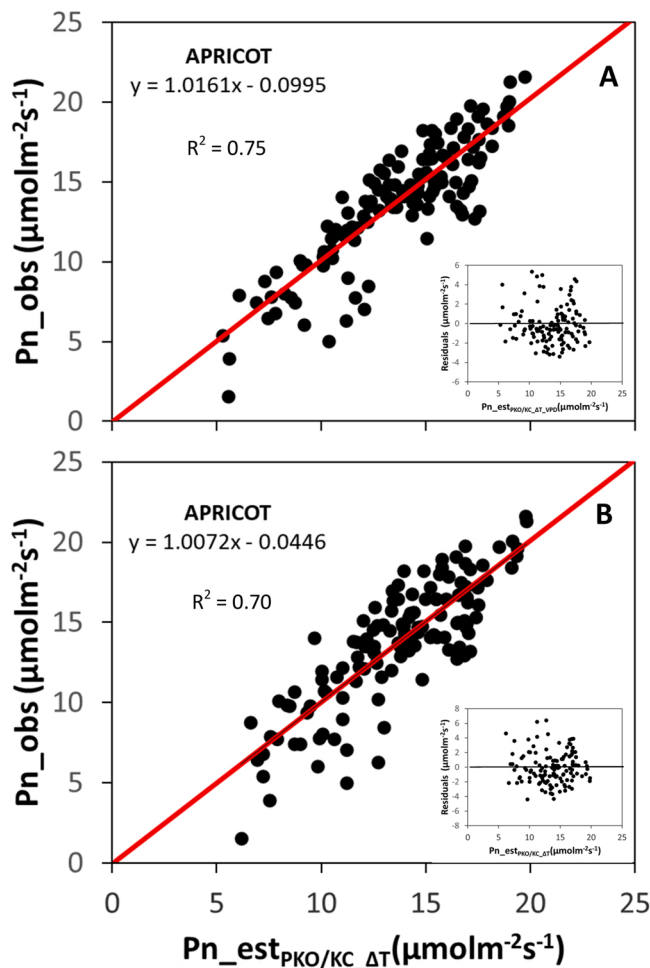**Fig. 6.** Relation between observed Pn (Pn_obs) and estimated with PKO/KC, ΔT and VPD as predictors (A) or removing VPD (B), in peach cv. "Calred". The complete dataset has been reported in the graphs (n = 128).

in comparison with the full irrigated treatments, not affecting productivity (Losciale et al., 2022). In general, Pn is affected by: (i) the amount of electrons exiting from the PSII and partly used for carboxylation; (ii) the carboxylative and photorespiratory activity of Rubisco, in turn dependent by leaf temperature; (iii) and by the amount of the entering CO_2, dependent by stomatal conductance and related to the leaf to air temperature difference (ΔT). $P_{KO/KC}$ variable integrates the amount of electrons exiting from the PSII (J_{PSII} measured by means of chlorophyll fluorescence protocols) and the carboxylative and photorespiratory activity of RuBisCO, strictly linked to the Michaelis-Menten activity of this enzyme for the two processes, in turn dependent by leaf temperature (von Caemmerer, 2000; Foyer et al., 2009). According to the principle of parsimony and considering that the same variables have been already selected for other species, linear regression models were finally performed using $P_{KO/KC}$, ΔT as predictors for Pn for "Primius" apricot and "Calred" peach. The resulting linear equations for apricot and peach were the following:

$$APRICOT : Pn_{(est)} = 5.86 + 0.19\left(P_{Ko/KC}\right) - 3.63(\Delta T) \tag{1}$$

$$PEACH : Pn_{(est)} = -2.42 + 0.30\left(P_{ko/kc}\right) - 1.84(\Delta T) \tag{2}$$

The standardized predictors coefficients (β), which consider the weight of each variable in the model regardless their order of magnitude, were 0.46 and -0.51 for $P_{KO/KC}$ and ΔT, respectively, in apricot and 0.75 ($P_{KO/KC}$) and -0.22 (ΔT) for peach.
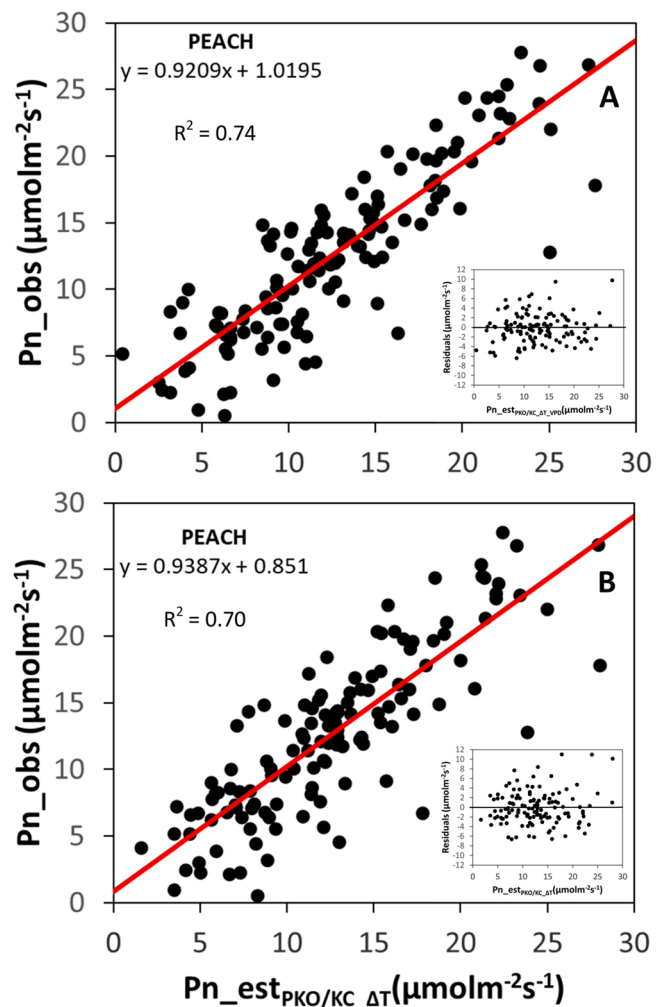
4.2.2. Stomatal conductance

The stepwise regression analysis for stomatal conductance estimation selected ΔT and VPD as predictors for both the species, with adjusted R^2 values of around 0.8 (Table 4). The Residual Prediction Deviation higher than 2 and between 1.4 and 2 for apricot and peach, respectively, during the validation step revealed an excellent/fair prediction performance of the models assessed. These results were further confirmed by the linear and the 1–1 relation between observed and estimated gs (Fig. 7). The following linear equations were established.

$$APRICOT : gs_{(est)} = 0.27 - 0.07(\Delta T) - 0.03(VPD) \tag{3}$$

$$PEACH : gs_{(est)} = 0.49 - 0.07(\Delta T) - 0.10(VPD) \tag{4}$$

with β of -0.88 and -0.38 for ΔT and VPD in apricot, and of -0.67 (ΔT) and -0.62 (VPD) for peach.

Even in this case the two variables selected had a clear physiological meaning in determining the degree of stomatal opening. The Vapour Pressure Deficit indicates the drying power of the atmosphere. The tree tried to cope with water loss modulating the stomatal closure. The leaf to air temperature difference is strictly linked to the passage of water from liquid to gaseous phase, thus also to the degree of the stomatal opening. Both the variables are used for assessing vegetative indices like the Crop Water Stress Index (Idso et al., 1981) and the Index of stomatal conductance (Jones, 1999; Ciccarese et al., 2011), strongly linked to the
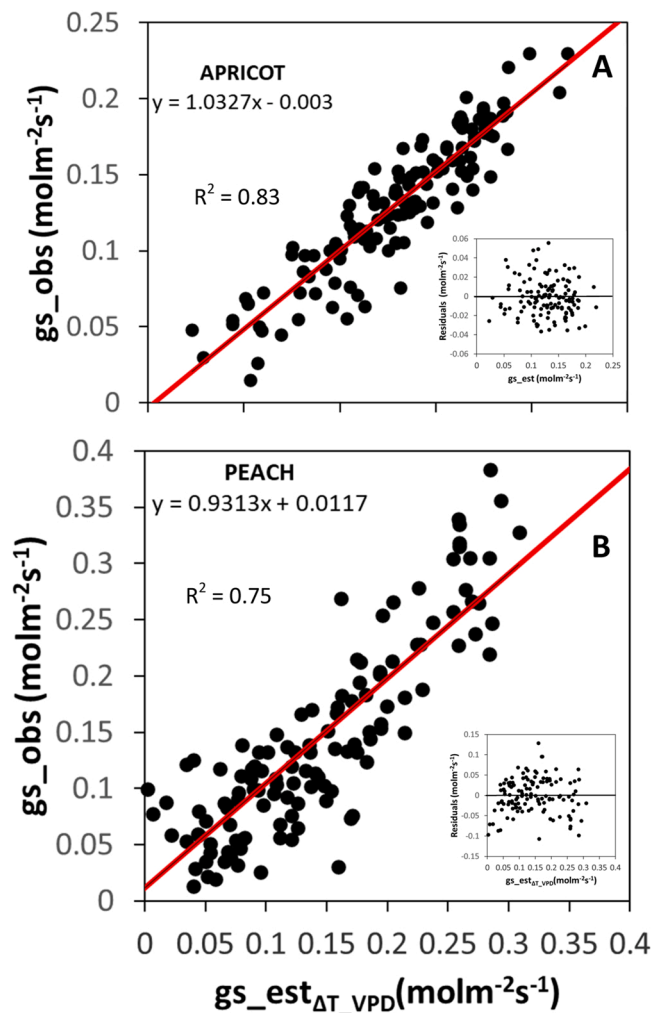
Fig. 7. Relation between observed gs (gs_obs) and estimated with ΔT and VPD as predictors in apricot cv. Primius (A) and in peach cv. Calred (B). The complete dataset has been reported in the graphs (n = 128).

Table 4
Prediction performances of the models for gs estimation, expressed as adjusted R^2 (Adj.R^2), Root Mean Square Error (RMSE) and Residual Prediction Deviation (RPD), obtained considering ΔT, VPD as predictors.

Step	Specie	Variable	Predictors (ΔT, VPD)
Training	Apricot cv. Primius	Adj.R^2	0.81
		RMSE	0.02
		RPD	2.36
	Peach cv. Calred	Adj.R^2	0.78
		RMSE	0.04
		RPD	2.08
Validation	Apricot cv. Primius	RMSE	0.02
		RPD	2.36
	Peach cv. Calred	RMSE	0.05
		RPD	1.77

plant water status.

5. Conclusions

"Primius", an early ripening apricot cultivar, behaved as a near-anisohydric plant, and vice versa "Calred", a late ripening peach cultivar, appeared to be near-isohydric. This knowledge could be interesting for choosing the tools for driving irrigation, accordingly. In "Primius", the information about stem water potential and soil water

content could be useful to drive irrigation since a good relationship with leaf functionality was found. On the other hand, the reduction of leaf functionality appeared weakly related to stem water potential in "Calred", suggesting that this index would be not so useful to drive irrigation in "pessimistic" genotypes. Another difference between the two genotypes was that in "Calred" peach, gs and Pn seemed to be more related to VPD than soil water content, while the opposite was observed in apricot. This knowledge could be useful to better manage the orchard. In "Primius" apricot, for example, soil water content should be maintained high in order to prevent a reduction of carbon fixation. In peach, in high water demanding environments, a moderate reduction of VPD could be positive for leaf photosynthesis and for the potential productivity.

The study aimed to identify a pool of indices that would describe the plant water status and the related performances. Net photosynthesis and stomatal conductance were chosen as candidate dependent variables summarizing the potential productivity of a tree. It was possible to identify two predictive variables ($P_{KO/KC}$, ΔT) that, arranged properly using a multivariate linear regression approach, were able to estimate net photosynthesis in both the genotypes under study. $P_{KO/KC}$ and ΔT meet the criteria previously described: physiological sound variables, quick to be measured, potentially implemented in a price affordable sensor. The measurement of these variables is faster than the direct detection of Pn with an Infra-red Gas analyzer Analyzer (IRGA) as chlorophyll fluorescence, leaf and air temperature could be acquired in less than 10 s per leaf instead of 3 min. At the moment, the simultaneous detection of these variables can be performed only proximally as $P_{KO/KC}$ requires the measurement of J_{PSII} in turn dependent on the measure of Fm'. This latter is obtained using a saturating light pulse and therefore it needs a proximal measurement. Vapour Pressure Deficit and ΔT were identified as stomatal conductance predictors, showing a satisfactory prediction performance. Also in this case, the selected variables had a well-known physiological meaning and their detection could be easy, inexpensive and gathered both proximally and remotely. Further research should be oriented at: managing irrigation considering the cultivar attitude and its relation with soil water content and air water demand; calibrating the models on other species; finding valid alternatives for Fm' estimation without the proximal measurement (i. e. the use of solar-induced chlorophyll fluorescence SIF could be interesting); and developing practical protocols using Pn and gs as Plant-Based Indicators for managing efficiently some agro-practices, first of all irrigation.

CRediT authorship contribution statement

Conceptualization and methodology, P.L.; data curation, P.L., M.C., A.M.S., C.G.; formal analysis, P.L., A.M.S., M.C.; investigation, L.G., M. C., C.G. R.L. L.T; methodology, P.L. and A.M.S.; supervision, P.L.; validation, P.L. and A.M.S.; writing original draft, P.L. and M.C.; Writing review and editing, P.L., A.M.S., M.C., L.G. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

References

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration: Guidelines for Computing Crop Water Require-ments. FAO Irrigation and Drainage, 1998. FAO, Rome, Italy. Paper No. 56.

Bastías, R.M., Losciale, P., Chieco, C., Corelli-Grappadelli, L., 2021. Red and blue netting alters leaf morphological and physiological characteristics in apple trees. art. 127 Plants 10. https://doi.org/10.3390/plants10010127.

Bellon-Maurel, V., Fernandez-Ahumada, E., Palagos, B., Roger, J.M., McBratney, A., 2010. Critical review of chemometric in-dicators commonly used for assessing the quality of the prediction of soil attributes by NIR spectroscopy. Trends Ann. Chem. 29, 1073–1081. https://doi.org/10.1016/j.trac.2010.05.006.

Bernacchi, C.J., Singsaas, E.L., Pimentel, C., Portis Jr, A.R., Long, S.P., 2001. Improved temperature response functions for models of RuBisCo-limited photosynthesis. Plant Cell Environ. 24, 253–259. https://doi.org/10.1111/j.1365-3040.2001.00668.x.

von Caemmerer, S., 2000. Chlorophyll fluorescence and oxygen exchange during C3 photosynthesis. CSIRO (ed) Biochemical Models of Leaf Photosynthesis. CSIRO Publishing, Australia, pp. 42–65.

Campi, P., Gaeta, L., Mastrorilli, M., Losciale, P., 2020. Innovative soil management and micro-climate modulation for saving water in peach orchards. art. 1052 Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.01052.

Cardenas-Lailhacar, B., Dukes, M.D., 2010. Precision of soil moisture sensor irrigation controllers under field conditions. Agric. Water Manag. 97 (5), 666–672. https://doi.org/10.1016/j.agwat.2009.12.009.

Chang, C.W., Laird, D.A., Mausbach, M.J., Hurburgh, C.R., 2001. Near-infrared reflectance spectroscopy–principal components regression analyses of soil properties. Soil Sci. Soc. Am. J. 65, 480–490. https://doi.org/10.2136/sssaj2001.652480x.

Chaves, M.M., 1991. Effects of water deficits on carbon assimilation. J. Exp. Bot. 42 (1), 1–16. https://doi.org/10.1093/jxb/42.1.1.

Cheng, L., Cheng, S., Shu, H., Luo, X., 1996. Effect of mild water stress in CO₂ assimilation and water use efficiency of field-grown peach trees. Acta Hortic. 374, 121–126. https://doi.org/10.17660/ActaHortic.1996.374.15.

Ciccarese, A., Stellacci, A.M., Tarricone, L., Gentilesco, G., Rubino, P. (2011). Physiological indicators of crop water status to optimize irrigation management in table grape. In Proceedings 17th International Symposium GiESCO, Asti-alba, Italy 29 august- 2 september 2011: 469–472. ISSN: 0369–8173.

Cifre, J., Bota, J., Escalona, J.M., Medrano, H., Flexas, J., 2005. Physiological tools for irrigation scheduling in grapevine (Vitis vinifera L.): an open gate to improve water-use efficiency? Agric. Ecosyst. Environ. 106 (2–3), 159–170. https://doi.org/10.1016/j.agee.2004.10.005.

Coupel-Ledru, A., Pallas, B., Delalande, M., Boudon, F., Carrié, E., Martinez, S., Regnard, J.L., Costes, E., 2019. Multi-scale high-throughput phenotyping of apple architectural and functional traits in orchard reveals genotypic variability under contrasted watering regimes. art. no. 52 Hortic. Res. 6 (1). https://doi.org/10.1038/s41438-019-0137-3.

Diaz-Espejo, A., 2013. New challenges in modelling photosynthesis: temperature dependencies of RuBisCo kinetics. Plant Cell Environ. 36, 2104–2107. https://doi.org/10.1111/pce.12192.

Fernández, J.E., 2014. Plant-based sensing to monitor water stress: applicability to commercial orchards. Agr. Water Manag. 142, 99–109. https://doi.org/10.1016/j.agwat.2014.04.017.

Fernández, J.E., 2017. Plant-based methods for irrigation scheduling of woody crops. art. 35 Horticulturae 3 (2). https://doi.org/10.3390/horticulturae3020035.

Flexas, J., Medrano, H., 2002. Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. Ann. Bot. 89, 183–189. https://doi.org/10.1093/aob/mcf027.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. Funct. Plant Biol. 29, 461–471. https://doi.org/10.1071/PP01119.

Foyer, C.H., Harbinson, J., 1994. Oxygen metabolism and the regulation of photosynthetic electron transport. In: Foyer, C.H., Mullineaux, P.M. (Eds.), Causes of pho-tooxidative stress and amelioration of defense systems in plants, 1994. CRC Press, Boca Raton FL, pp. 1–42.

Foyer, C.H., Bloom, A.J., Queval, G., Noctor, G., 2009. Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. Annu. Rev. Plant Biol. 60, 455–484. https://doi.org/10.1146/annurev.arplant.043008.091948.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92. https://doi.org/10.1016/S0304-4165(89)80016-9.

Hernandez-Santanaa, V., Fernández, J.E., Diaz-Espejo, A., 2019. Irrigation scheduling in a high-density olive orchard from estimated stomatal conductance. Acta Hortic. 1253, 449–456 https://doi.org/10.17660/ActaHortic.2019.1253.59.

Idso, S.B., Jackson, R.D., Pinter Jr., P.J., Reginato, R.J., Hatfield, J.L., 1981. Normalizing the stress degree day for environmental variability. Agric. Meteorol. 24, 45–55. https://doi.org/10.1016/0002-1571(81)90032-7.

Jones, H.G., 1999. Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. Plant Cell Environ. 22 (9), 1043–1055. https://doi.org/10.1046/j.1365-3040.1999.00468.x.

Jones, H.G., 2004. Irrigation scheduling: advantages and pitfalls of plant-based methods. J. Exp. Bot. 55, 2427–2436. https://doi.org/10.1093/jxb/erh213.

Lakso, A.N., Santiago, M., Stroock, A.D., 2022. Monitoring stem water potential with an embedded microtensiometer to inform irrigation scheduling in fruit crops. Horticulturae 2022 (8), 1207. https://doi.org/10.3390/horticulturae8121207.

Laurens, F., Aranzana, M.J., Arus, P., Bassi, D., Bink, M., Bonany, J., Caprera, A., Corelli-Grappadelli, L., Costes, E., Durel, C.E., Mauroux, J.B., Muranty, H., Nazzicari, N., Pascal, T., Patocchi, A., Peil, A., Quilot-Turion, B., Rossini, L., Stella, A., Troggio, M., Velasco, R., Van De Weg, E., 2018. An integrated approach for increasing breeding efficiency in apple and peach in Europe. art. no. 11 Hortic. Res. 5 (1). https://doi.org/10.1038/s41438-018-0016-3.

Lauri, P.E., Barigah, T.S., Lopez, G., Martinez, S., Losciale, P., Zibordi, M., Manfrini, L., Corelli-Grappadelli, L., Costes, E., Regnard, J.L., 2016. Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. Trees - Struct. Funct. 30 (5), 1893–1908. https://doi.org/10.1007/s00468-016-1408-3.

Levidow, L., Zaccaria, D., Maia, R., Vivas, E., Todorovic, M., Scardigno, A., 2014. Improving water-efficient irrigation: Prospects and difficulties of innovative practices. Agr. Water Manag. 146, 84–94. https://doi.org/10.1016/j.agwat.2014.07.012.

Levin, A., Nackley, L., 2021. Principles and practices of plant-based irrigation management. HortTechnology 31 (6), 650–660. https://doi.org/10.21273/HORTTECH04862-21.

Losciale, P., Chow, W.S., Corelli-Grappadelli, L., 2010. Modulating the light environment with the peach 'asymmetric orchard': effects on gas exchange performances, photoprotection, and photoinhibition. J. Exp. Bot. 61, 1177–1192. https://doi.org/10.1093/jxb/erp387.

Losciale, P., Zibordi, M., Manfrini, L., Corelli-Grappadelli, L., 2008. Effects of rootstock on pear photosynthetic efficiency. Acta Hortic. 800, 241–247. https://doi.org/10.17660/ActaHortic.2008.800.28.

Losciale, P., Hendrickson, L., Corelli-Grappadelli, L., Chow, W.S., 2011a. Quenching partitioning through light-modulated chlorophyll fluorescence: a quantitative analysis to assess the fate of the absorbed light in the field. Environ. Exp. Bot. 73, 73–79. https://doi.org/10.1016/j.envexpbot.2010.10.024.

Losciale, P., Gaeta, L., Manfrini, L., Tarricone, L., Campi, P., 2020. Orchard floor management affects tree functionality, productivity and water consumption of a late ripening peach orchard under semi-arid conditions. art. 8135 Appl. Sci. 10. https://doi.org/10.3390/app10228135.

Losciale, P., Manfrini, L., Morandi, B., Zibord, I.M., Corelli-Grappadelli, L., 2022. A plant-based index for plant water status detection and irrigation scheduling in pear 'Abbé Fetel': first results on the use of the I$_{PL}$ index. Acta Hortic. 1335, 311–316. https://doi.org/10.17660/ActaHortic.2022.1335.38.

Losciale, P., Zibordi, M., Manfrini, L., Morandi, B., Bastias, R.M., Corelli-Grappadelli, L., 2011b. Light management and pho-toinactivation under drought stress in Peach. Acta Hortic. 922, 341–348. https://doi.org/10.17660/ActaHortic.2011.922.44.

Losciale, P., Manfrini, L., Morandi, B., Pierpaoli, E., Zibordi, M., Stellacci, A.M., Salvati, L., Corelli-Grappadelli, L., 2015. A multivariate approach for assessing leaf photo-assimilation performance using the IPL index. Physiol. Plant. 154, 609–620. https://doi.org/10.1111/ppl.12328.

Losciale, P., Manfrini, L., Morandi, B., Novak, B., Pierpaoli, E., Zibordi, M., Corelli-Grappadelli, L., Anconelli, S., Galli, F., 2014. Water restriction effect on pear rootstocks: photoprotective processes and the possible role of photorespiration in limiting carbon assimilation. Acta Hortic. 1058, 237–244. https://doi.org/10.17660/ActaHortic.2014.1058.27.

Loveys, B.B., Robinson, S.P., Downton, W.J.S., 1987. Seasonal and Diurnal Changes in Abscisic Acid and Water Relations of Apricot Leaves (Prunus armeniaca L.). New Phytol. 107 (1), 15–27.

Manfrini, L., Losciale, P., Morandi, B., Pierpaoli, E., Zibordi, M., Anconelli, S., Galli, F., Corelli Grappadelli, L., 2018. A multi-tool approach for assessing fruit growth, production and plant water status of a pear orchard. Acta Hortic. 1197, 97–102. https://doi.org/10.17660/ActaHortic.2018.1197.13.

Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence – a practical guide. J. Exp. Bot. 51, 659–668. https://doi.org/10.1093/jexbot/51.345.659.

Murata, N., Nishiyama, Y., 2018. ATP is a driving force in the repair of photosystem II during photoinhibition. Plant Cell Environ. 41, 285–299. https://doi.org/10.1111/pce.13108.

Naor, A., 2006. Irrigation scheduling and evaluation of tree water status in deciduous orchards. Hortic. Rev. 32, 111–165. https://doi.org/10.1002/9780470767986.ch3.

Naor, A., Klein, I., Doron, I., 1995. Stem water potential and apple size. J. Am. Soc. Hortic. Sci. 120, 577–582. https://doi.org/10.21273/JASHS.120.4.577.

Osmond, C.B., Grace, S.C., 1995. Perspectives on photoinhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis? J. Exp. Bot. 46, 1351–1362. https://doi.org/10.1093/jxb/46.special_issue.1351.

Pagay, V., 2022. Evaluating a novel microtensiometer for continuous trunk water potential measurements in field-grown irrigated grapevines. Irrig. Sci. 40, 45–54. https://doi.org/10.1007/s00271-021-00758-8.

Ruiz-Sánchez, M.C., Domingo, R., Pérez-Pastor, A., 2007. Daily variations in water relations of apricot trees under different irrigation regimes. Biol. Plant. 51, 735–740. https://doi.org/10.1007/s10535-007-0150-5.

Schultz, H.R., 2003. Differences in hydraulic architecture account for nearisohydric and anisohydric behaviour of two field-grown Vitis vinifera L. cultivars during drought. Plant Cell Environ 26, 1393–1405.

Seaton, G.G.R., Walker, D.A., 1990. Chlorophyll fluorescence as a measure of photosynthetic carbon assimilation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 242, 29–35. https://doi.org/10.1098/rspb.1990.0099.

Snyder, R.L., 2017. Climate change impacts on water use in horticulture. Horticulturae 3, 27–35. https://doi.org/10.3390/horticulturae3020027.

Socías, X., Correia, M.J., Chaves, M., Medrano, H., 1997. The role of abscisic acid and water relations in drought responses of subterranean clover. J. Exp. Bot. 48 (6), 1281–1288. https://doi.org/10.1093/jxb/48.6.1281.

Soulis, K.X., Elmaloglou, S., Dercas, N., 2015. Investigating the effects of soil moisture sensors positioning and accuracy on soil moisture based drip irrigation scheduling systems. Agric. Water Manag. 148, 258–268. https://doi.org/10.1016/j. agwat.2014.10.015.

Steinberg, S.L., McFarland, M.J., Miller Jr, J.C., 1989. Effect of water stress on stomatal conductance and leaf water relations on leaves along current-year branches of peach. Aust. J. Plant Physiol. 16, 549–560.

Stöckle, C.O., Marsal, J., Villar, J.M., 2011. Impact of climate change on irrigated tree fruit production. Acta Hortic. 889, 41–52. https://doi.org/10.17660/ ActaHortic.2011.889.2.

Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evapo-rative demand: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 49, 419–432. https://doi.org/10.1093/jxb/49. Special_Issue.419.

Torrecillas, A., Galego, R., Péerez-Pastor, A., Ruiz-Sánchez, M.C., 1999. Gas exchange and water relations of young apricot plants under drought conditions. J. Agric. Sci. 132 (4), 445–452. https://doi.org/10.1017/S0021859699006577.

Turner, N., Schulze, E.D., Gollan, T., 1985. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. Oecologia 65 (3), 348–355. http://www.jstor.org/stable/4217539.

Xiloyannis, C., Uriu, K., Martin, G.C., 1980. Seasonal and diurnal variations in absicic acid, water potential, and diffusive resistance in leaves from irrigated and non-irrigated peach trees. J. Am. Soc. Hortic. Sci. 105, 412–415, 1980.

Yang, Z., Tian, J., Feng, K., Gong, X., Liu, J., 2021. Application of a hyperspectral imaging system to quantify leaf-scale chlorophyll, nitrogen and chlorophyll fluorescence parameters in grapevine. Plant Physiol. Biochem. 166, 723–737. https://doi.org/10.1016/j.plaphy.2021.06.015.

Yi, X.P., Yao, H.S., Fan, D.Y., Zhu, X.G., Losciale, P., Zhang, Y.L., Zang, W.F., Chow, W.S., 2022. The energy cost of repairing photoinactivated Photosystem II: an experimental determination in cotton leaf discs. N. Phytol. 235, 446–456. https://doi.org/ 10.1111/nph.18165.

Zhang, Q., Chen, Y., Xiong, Y., Moritani, S., Wu, X., Yan, C., Chen, X., 2021. Which is more sensitive to water stress for irrigation scheduling during the maturation stage: grapevine photosynthesis or berry size? Atmosphere 2021 (12), 845. https://doi. org/10.3390/atmos12070845.