RESEARCH PAPER

Modulating the light environment with the peach ‘asymmetric orchard’: effects on gas exchange performances, photoprotection, and photoinhibition

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Abstract

The productivity of fruit trees is a linear function of the light intercepted, although the relationship is less tight when greater than 50% of available light is intercepted. This paper investigates the management of light energy in peach using the measurement of whole-tree light interception and gas exchange, along with the absorbed energy partitioning at the leaf level by concurrent measurements of gas exchange and chlorophyll fluorescence. These measurements were performed on trees of a custom-built ‘asymmetric’ orchard. Whole-tree gas exchange for north–south, vertical canopies (C) was similar to that for canopies intercepting the highest irradiance in the morning hours (W), but trees receiving the highest irradiance in the afternoon (E) had the highest net photosynthesis and transpiration while maintaining a water use efficiency (WUE) comparable to the other treatments. In the W trees, 29% and 8% more photosystems were damaged than in C and E trees, respectively. The quenching partitioning revealed that the non-photochemical quenching (NPQ) played the most important role in excess energy dissipation, but it was not fully active at low irradiance, possibly due to a sub-optimal trans-thylakoid ΔpH. The non-net carboxylative mechanisms (NC) appeared to be the main photoprotective mechanisms at low irradiance levels and, probably, they could facilitate the establishment of a trans-thylakoid ΔpH more appropriate for NPQ. These findings support the conclusion that irradiance impinging on leaves may be excessive and can cause photodamage, whose repair requires energy in the form of carbohydrates that are thereby diverted from tree growth and productivity.

Key words: Chlorophyll fluorescence, D1 protein, non-net carboxylative transports, non-photochemical quenching, photodamage, photosynthesis, quenching analysis, whole canopy gas exchange.

Introduction

The energetic basis of orchard productivity lies in the interaction between the tree and sunlight. The amount of dry matter produced by a tree is linearly related to the amount of light it intercepts (Monteith, 1977; Lakso, 1994). This concept drove the evolution of modern, intensive orchard systems (Corelli Grappadelli and Lakso, 2007), which aim to cover the ground as soon as possible with a photosynthetic surface in order to increase light interception, while maintaining good light distribution throughout the canopy, to improve fruit quality and flower bud differentiation (Palmer, 1980). Several authors have documented a direct relationship between planting density and fruit yield (t ha⁻¹) as a consequence of an increased leaf area index (LAI) and thus orchard light interception (Guerriero et al., 1980; Hutton et al., 1987; Chalmers and van den Ende, 1989; Loreti et al., 1989; Caruso et al., 2000; Corelli Grappadelli et al., 2000; Nuzzo et al., 2002). However, a direct relationship between irradiance and productivity is not always recorded. No difference for orchard yield was found, for example, on peach cv. Ross
trained as Cordon or Kearney Agricultural Center Perpendicu-
dicular V (KAC-V) at 1196 trees per hectare, even though the Cordon training system intercepted more light than the KAC-V (Grossman and De Jong, 1998).

Light provides energy for electron transport, generating ATP and reducing power (NADPH) used in the Calvin–Benson cycle for carboxylation. Leaf net photosynthesis increases with irradiance until a saturation point is reached, beyond which no improvement is found for further increases in irradiance (Bohning and Burns, 1956). The saturation point can be different between plant species and is affected by plant nutritional and water status, light environment during leaf growth, and leaf age. (Escalona et al., 1999; Iacono and Sommer, 1999; Cheng et al., 2001; Greer and Halligan, 2001). In peach (Prunus persica L.) the saturation point is normally reached at about 700–900 µmol photons m⁻² s⁻¹ (Kappel and Flore, 1983; Gaudillere and Moing, 1992). In several parts of the world, under clear sky conditions irradiance commonly reaches 2000 µmol photons m⁻² s⁻¹ or above (Nobel, 2005a); therefore, for photosynthesis at leaf level, about half the available light may be in excess (Corelli Grappadelli and Lakso, 2007). Ameliorating effects have actually been found in the photosynthetic performance of apple (Malus × domestica Borkh) and grapefruit (Citrus paradisi L.) by reducing (excessive) light interception with light-reflective kaolin particles sprayed on the leaves (Glenn et al., 2001; Jifon and Syvertsen, 2003).

At the whole tree level, however, the saturation point is not always easily detectable. The genetically dwarf peach cv. Valley Red did not reach a steady-state when photosynthesis was measured on entire trees (Corelli Grappadelli et al., 1996). On the other hand, in grapefruit, trees covered with 30% and 60% shading assimilated more dry matter than non-shaded ones (Raveh et al., 2003). Whole plant gas exchange measurements carried out on apple trees sprayed with kaolin showed that, by reducing light and canopy temperature, net photosynthesis increased in response to the reduced environmental stress (Glenn et al., 2003).

The energy absorbed by a leaf is managed through several competing pathways involving thermal processes, fluorescence, and photochemistry. The main purposes of these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy these pathways are photosynthetic carboxylation and the dissipation of excess energy to limit the formation of reactive oxygen species (ROS). ROS react with and destroy...
multi-pronged strategy for photoprotection and recovery with mutual support from the several processes involved. There is an energetic price to pay for this capability. These processes use reducing power and decrease net photosynthetic efficiency, since some intercepted photons are not used for carboxylation, but also because fixed CO$_2$ and reducing power are lost (Foyer and Harbinson, 1994).

Managing the energy captured by the tree is of great interest among scientists who look to increase the diminutive 5–10% of the absorbed energy in full light that plants are able to use for net carboxylation (Long et al., 1994). In such a situation, even small changes in carboxylation efficiency and photosynthate allocation could modify the primary net and commercial plant productivity (Flore and Lakso, 1988).

The first objective of this study was to investigate, at the whole plant level, the relationship between the light environment and photosynthetic performance, water use, and PSII damage in peach. Once the response of the whole canopy carbon assimilation to irradiance was assessed, the study focused on the management of the absorbed energy, studying the partitioning of energy into the several utilization (i.e. net photosynthesis), and photoprotection pathways. This last investigation was performed only at a single leaf level since the energy partitioning approach at a whole canopy scale is still difficult.

**Materials and methods**

**Plant material**

The trials were carried out in 2006 at the University of Bologna Experiment Farm in Cadriano, Bologna, on three-year-old trees of the nectarine (Prunus persica (L.) Batsch var. laevis) cv. Alice col., grafted onto a GF305 rootstock with 5 m between the rows. The spacing is variable along the row, depending on the treatment. This cultivar exhibits a pillar growth habit naturally forming spindle-type canopies. The orchard is called ‘asymmetric’ because the rows vary in orientation and inclination, forming three different patterns of light interception during the day, two of which are asymmetric around solar noon. In addition to vertical, N–S (0–180°) oriented trees constituting the control (C), rows are either 330–150° (E) or 30–210° (W) oriented. The trees in the former are planted with canopies 30° slanting towards East, thus facing West, and trees from the latter are mirroring them, as they are planted with a canopy inclination 30° towards West, thus facing East (Fig. 1). The orchard consists of three plots, each containing one replicate of the three orientation/inclination combinations of 40–50 plants. Along the N–S oriented rows trees are spaced 1.2 m apart, and 1 m in the W and E treatments. The goal of this tree arrangement was to obtain three different light environments at the same time of day without modifying the overall climatic conditions.

**Whole plant measurements**

Two plants with similar vigour and crop load were chosen for each treatment. During fruit cell expansion (ST-III), when shoot growth had stopped, daily light interception was measured for each tree on a clear day using a custom-built light scanner (Giuliani et al., 2000). The scanner was made up of a metal bar combining 48 irradiance sensors (NPN Silicon phototransistor P800, TRW Optron, TRW Inc., Carrolton, Texas, USA) spaced 0.05 m apart. Incoming irradiance was measured on unobstructed ground; subsequently, the scanner was moved under the tree, parallel to the row for a length encompassing all the area shaded by the canopy, recording data every 0.2 m. Since the phototransistors used have a spectral response in the wavelength range 300–1100 nm, the fraction of light measured by the sensor in the visible light range (400–700 nm) was calculated according to Giuliani et al. (2000) in their Appendix 1. The irradiance measured by each sensor was considered as representative of the direct and diffuse irradiance falling on an area of 0.01 m$^2$ (0.05×0.2 m) surrounding that sensor. The difference between the incoming full light and that reaching the ground under the trees equals the total light flux intercepted by the plant (μmol photons m$^{-2}$ s$^{-1}$).

Leaf area per tree was estimated by a calibration equation obtained by plotting area against dry weight of an increasing number of leaves for each tree. Before the end of the season all the leaves of each plant were detached while still full green and their dry weight was measured and converted to leaf area.

At ST-III and post-harvest (PHV), whole-canopy gas exchange was monitored using a custom-built open system, modelled after that described by Corelli Grappadelli and Magnanini (1993, 1997), with some modifications. Six polyethylene chambers were built, each enclosing one tree for 6 d and 8 d in ST-III and PHV, respectively. Air was forced through each assimilation chamber by a fan and the flow of air was measured by a custom-built flow gauge, calibrated using the standard gas method reported by Corelli Grappadelli and Magnanini (1993). The flow provided a full chamber volume exchange every 2–3 min, thus keeping the air temperature inside the chamber quite comparable to that outside (Corelli Grappadelli and Magnanini, 1993). Each flow gauge was connected to a CR10X datalogger (Campbell Scientific...
L. Leicestershire, UK), continuously monitoring the flow rate. A sample of gas from the inlet and outlet manifolds was drawn through PVC tubes to an infrared gas analyser (IRGA) (CIRAS SC, PP Systems, Hitchin, UK), for CO₂ (ppm) and H₂O (mbar) determination. The CR10X datalogger also controlled the operation of a bench of solenoid valves which switched the inlet and outlet flows from each chamber to the IRGA. A complete set of readings for each plant included the measurement of water vapour pressure and CO₂ concentration at the inlet and outlet of the chamber and the amount of air flowing through that chamber. Each plant was monitored every 15 min. Whole- canopy net carbon and water exchange rate was calculated by multiplying the CO₂ and H₂O differential between the inlet and the outlet of each chamber by the molar flow through the chamber (obtained from the measured flow, corrected for inlet air temperature). Dividing the gas exchange parameters by the total leaf area the specific net CO₂ uptake (NCU, μmol CO₂ m⁻² s⁻¹), the specific transpiration (TRₚₑₚ, L H₂O m⁻² h⁻¹) and the derived water use efficiency (WUE, mol l⁻¹) were obtained, and hourly averages were computed for each chamber. Since gas exchange parameters are strictly related to the environmental conditions (particularly to solar radiation), clear days with similar radiative profiles were chosen for the present analysis. Incident light energy density flux (W m⁻²) was measured using a pyranometer attached to a weather station (AdCon telemetry GmbH, Austria) placed near the orchard.

To estimate the daily cumulative gross damage of PSII on each plant, fully expanded leaves, collected at predawn when almost all the PSII are fully functional, were used to calculate the quantum yield of photooinactivation (Qᵥ). Leaf discs were floated with their abaxial side up, in order to facilitate gas exchange (Sun et al., 1994) for 2 h in darkness. They continued to float with the abaxial side up on the lincomycin solution (an inhibitor of the D1 protein repair; Aro et al., 1994) for 45 min of dark exposure, the product of irradiance and time of exposure (mol photons m⁻² s⁻¹) was used as the independent variable. Before the photoinhibitory treatment, six leaf discs (three for each irradiance) were used as non-photoinhibited control, on both leaf sides after 45 min of dark exposure. The absolute functional PSII content can be calculated for each plant. This is a simplification as the Qᵥ calculated at optimal and steady temperature in the laboratory may be an underestimation of the quantum yield of photooinactivation occurring in the field, where the photodamage process should proceed faster as the temperature stresses are greater (Yamamoto et al., 2008).

Single leaf measurements

During fruit cell division (ST-I), stone hardening (ST-II), cell extension (ST-III), and post-harvest (PHY) six attached, well-explored leaves were selected on the East and West side of C, W and E trees. Irradiance (μmol photons m⁻² s⁻¹), leaf and air temperature (°C), gas exchange, and chlorophyll fluorescence parameters, used for the energy partitioning analysis, were measured on the leaves four times during the day (between 09.00 h and 17.00 h) using an open circuit infrared gas exchange system fitted with a leaf fluorimeter and a light sensor (Li-Cor 6400, Li-Cor inc., Lincoln Nebraska USA). Illumination was supplied by an artificial LED light source whose intensity was set equal to the natural irradiance measured next to the leaf lamina immediately before measurement. The maximum quantum yield of photosystem II (F₀/Fₘ) was measured predawn, after complete relaxation of the photosystems and after recovery during the night (Hikosaka et al., 2004).

Analysis of the partitioning of excitation energy

Quenching analysis was carried out using the model by Hendrickson et al. (2004), combined with the photosynthesis model proposed by von Caemmerer (2000). Setting the total amount of energy absorbed by photosystems equal to 1.0:

Φₐ₃ = F₀/Fₘ = the combined quantum efficiency of fluorescence and constitutive thermal dissipation, where F₀ is the steady-state fluorescence for a light-adapted leaf and Fₘ is the maximum chlorophyll fluorescence after a saturating pulse for a dark-adapted leaf. Variations in irradiance do not alter this parameter appreciably (Hendrickson et al., 2004);

Φₙ₉₂ = (Fₛₐₚₙ/F₀) - (Fₛₐₚₙ/Fₘ) is the quantum efficiency of light-dependent thermal dissipation, where Fₘ is the maximum chlorophyll fluorescence after a saturating pulse for a light-adapted leaf. The light-dependent thermal dissipation is mainly promoted by the photoprotective non-photochemical quenching via the xanthophyll cycle and associated with the potential photoactivated PSII;

Φₚₛₛᵢᵣ = 1 - (Fₛₐₚₙ/Fₘ) is the quantum efficiency of photochemical transports used for photosynthesis, photosorerespiration, mitochondrial respiration, and alternative transports (water–water cycle, cyclic transport around PSI, and the glutathione–ascorbate cycle).

To allow comparisons among all the energetic components, data were expressed as electron transport rates J (μmol e⁻ m⁻² s⁻¹) by multiplying each quantum efficiency (Φₐ₃, Φₙ₉₂, Φₚₛₛᵢᵣ) by the estimated total amount of electrons that can be displaced by the absorbed irradiance:

Jₜₒᵣᵣ = 0.5 × 0.85 × irradiance, where the coefficient 0.5 takes into account that one electron is moved by two photons (one photon absorbed by each photosystem; Melis et al., 1987) and 0.85 is the average leaf absorptance (Ehleringer and Pearcy, 1983; Krall and Edwards, 1992; Schultz, 1996).

Through gas exchange measurements, Jₛₛᵢᵣ could be partitioned into several components:

Jₛₛᵣₒ = Pₑ × 4 is the net photosynthesis expressed as electron transport rate, where Pₑ is the net carbon assimilation (μmol CO₂ m⁻² s⁻¹) multiplied by four electrons sequestered for carboxylating one molecule of CO₂.

of photooinactivation of PSII (μmol PSII mol⁻¹ photons). Multipling Qᵥ by the photon exposure intercepted per unit leaf area gives an estimation of the amount of damaged PSII (μmol PSII m⁻²) over time (Hendrickson et al., 2004). Daily cumulative PSII damage was estimated using the quantum yield of photooinactivation, the intercepted daily photon exposure and the total leaf area measured on each plant. This is a simplification as the Qᵥ calculated at optimal and steady temperature in the laboratory may be an underestimation of the quantum yield of photooinactivation occurring in the field, where the photodamage process should proceed faster as the temperature stresses are greater (Yamamoto et al., 2008).

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patterns of net carbon uptake showed an increase for all treatments until 11.00 h with no differences revealed. The E treatment showed a further NCU increase, reaching the maximum value at 12.00 h and remaining at this level until 14.00 h, after which E net photosynthesis gradually decreased. W and C net CO2 fixation diminished after 11.00 h and no difference was detected between these two treatments. C showed lower values than E at 12.00 h and at 13.00 h, while excluding values recorded at 15.00 h. W net photosynthesis was lower than E from 13.00 h until 17.00 h. At 18.00 h, NCU became similar among the three treatments (Fig. 3A). Transpiration (TRWP) increased until 11.00 h without any difference among treatments. W canopies reached the maximum value at 11.00 h with a subsequent decrease during the afternoon, while C and E continued to increase their transpiration reaching the maximum at 14.00 h; afterwards, TRWP decreased. Despite the fact that the maximum values were reached at two different times of the day, C and W transpiratory losses remained quite similar, even in the afternoon, and were lower than E until 14.00 h. Afterwards, a difference was recorded between E and W and, at 19.00 h, canopy transpiration was similar among treatments (Fig. 3B). Water use efficiency declined during the day, starting from the maximum value recorded at 06.00 h and reaching a steady-state at 12.00 h; no differences were recorded among treatments (Fig. 3C).

At post-harvest, net photosynthesis increased during the morning until 08.00 h, maintaining quite similar values until 10.00 h. No differences were recorded among treatments. After 10.00 h, net photosynthesis decreased in C and W canopies reaching minimum values at 18.00 h. At 15.00 h and at 16.00 h W net uptake was lower than C values (Fig. 3D). After 10.00 h, NCU of E trees continued to increase, reaching the maximum at 13.00 h; afterwards it decreased, reaching the minimum at 18.00 h. Excluding values recorded at 18.00 h, in the afternoon E trees showed higher NCU than the other two treatments (Fig. 3D).
canopy transpiration increased during the morning with no difference among the treatments. W reached the maximum value at 10.00–11.00 h; afterwards a rapid decrease was observed. In C trees $TR_{WP}$ peaked at 10.00 h, maintained a steady-state until 15.00 h, and then decreased. Transpiration of E trees increased until 14.00 h, decreasing afterwards. In the afternoon, C transpiration was higher than W from 15.00 h until 17.00 h, although E trees showed the highest $TR_{WP}$ (Fig. 3E). Also post-harvest, the water use efficiency was similar among treatments (Fig 3F). The maximum value was recorded in the early morning and decreased reaching a minimum, steady $WUE$ at 12.00 h.

The functional PSII absolute content of non-photoinhibited samples was about 1.12 μmol PSII m$^{-2}$. This content of active PSII was sustained during the day, as photoactivated PSII complexes were repaired quickly by D1 protein synthesis. Upon inhibiting the D1 protein synthesis, however, the functional PSII fraction decayed exponentially with an increase in photon exposure (data not shown); the calculated maximum quantum yield of photoinactivation of PSII ($Q_y$) for a 100% active PSII population was 0.07 μmol PSII mol$^{-1}$ photons. Multiplying this quantum yield of photoinactivation by the cumulative photon exposure through the day gives the cumulative gross content of photodamaged PSII.

At each measurement, W trees showed a higher cumulative PSII damage than the other samples, while, in the morning, the inactive PSII centres were similar between C and E. In the afternoon, the increase in cumulative content of damaged PSII in E was more rapid, such that at 17.00 h the cumulative gross content of damaged PSII was 0.62, 0.44, and 0.57 μmol PSII m$^{-2}$, in W, C, and E samples, respectively, with the W trees having 8% and 29% more cumulative gross damage than E and C, respectively (Fig. 4).

**Single leaves**

Measurements were performed on 16 May, 12–13 June, 4–5 July, and 10 August in Stages I, II, III, and post-harvest, respectively. The irradiance changed during the day in the three canopies from ~150 to ~2100 μmol photons m$^{-2}$ s$^{-1}$.

The multivariate principal component analysis (PCA) showed that the first two calculated eigenvalues explained data sorting by more than 80%. This percentage fell under 70% only in ST-III (Fig. 5). In the four stages a significant, positive relation was found among $J_{F_D}$, $J_{NPQ}$, $J_{NC}$, and irradiance (Fig. 5), and these four parameters heavily characterized the gradient represented by Factor I (factor...
loading, $r > 0.9$). This explained data sorting for more than 50% in all stages except ST-III (~45%). Stomatal conductance ($g_s$) was highly correlated to Factor 2 ($r > 0.8$) except in Stage III, where $g_s$ did not show any correlation with both principal components (Fig. 5C) and the calculated factor loadings were 0.4 and 0.2 for Factor 1 and 2, respectively. Air temperature, leaf temperature, and the vapour pressure deficit were more correlated to the second component than to Factor 1. $T_{air}$, $T_{lf}$, and $VPD$ were positively related, while a negative correlation with stomatal conductance was found in ST-I, ST-II, and PHV (Fig. 5A, B, D). In all stages the correlation between $J_{CO_2}$ and Factor 1 was higher than with the second. Although significant factor loadings ($r > 0.9$) were recorded in ST-II and PHV, in the remaining two stages this parameter never exceeded 0.8. The $J_{CO_2}$/Factor 2 correlation was never significant; however, $J_{CO_2}$, $J_R$, and especially $J_{AT}$ showed the highest correlation with Factor 2 among all electron transport rates (Fig. 5). The all measured cases projection on the main factor axes showed a strong

![Fig. 4.](image) Cumulative PSII inactivation estimated on W (white bars), E (dashed bars), and C (grey bars) trees. Each point represents the average of two measurements $\pm$SE. The active PSII content for non-photoinhibited samples was about 1.12 $\mu$mol m$^{-2}$. 

![Fig. 5.](image) Multivariate principal component analysis performed for ST-I (A), ST-II (B), ST-III (C), and PHV (D). Each of the 13 variables is represented by a vector, and its direction and length indicates the variable's contribution to the two principal factors. The longer and closer each vector is to the factor axis, the greater its contribution to determine the principal component.
overlapping between W, E, and C cases (Fig. 6). The three treatments did not influence the order of cases disposition along these gradients (Factor 1–2), therefore this classification was abandoned in order to study the general relationship existing between the \( J \) parameters and irradiance.

The energy used in the several dissipating processes was expressed as equivalent electron transport rate and plotted against irradiance for each stage. \( J_{\text{f,D}} \) increased linearly with irradiance (Fig. 7), while in all the stages \( J_{\text{NPQ}} \) increased following an expo-linear pattern, with rapidly increasing response until 800–1000 \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \), when the maximum slope was attained and the energy dissipated as heat started to increase linearly with irradiance (Fig. 8). The rate of electron transport exiting PSII (\( \mu \text{mol e}^{-} \text{m}^{-2} \text{s}^{-1} \)) as a function of irradiance saturated at high irradiance for all the stages. The maximum slope was reached at the lowest irradiances and the electron transport rate used in photochemistry reached a saturation around 1000–1200 \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \) (Fig. 9). Partitioning \( J_{\text{NC}} \) allowed a calculation of the energy allocated to respiration/photorespiration (\( J_{\text{R}} \)) and to the alternative transports (\( J_{\text{AT}} \)). \( J_{\text{R}} \) was also directly related to irradiance. In ST-I and II a linear relation was recorded and a curvilinear one in ST-III. A curvilinear pattern was also found at post-harvest, although a considerable scatter was recorded (Fig. 10). In all the stages examined, the relation between the electron transport for the alternative transports (\( J_{\text{AT}} \)) and irradiance was not clear, although it increased reaching the highest values at middle-high irradiances (Fig. 10).

The integration of irradiance and the principal \( J \) parameters provided the amount of energy intercepted by leaves (\( \Sigma_{\text{PPFD}} \)) and devoted to photosynthesis (\( \sum_{e-(CO_2)} \)) or to the main dissipative mechanisms (\( \Sigma_{e-(f,D)} \), \( \Sigma_{e-(NPQ)} \), and \( \Sigma_{e-(NC)} \)) between 09.00 h and 17.00 h in the three treatments during two of the stages (ST-III and PHV) which were also tested by the whole canopy measurements (Table 1). W leaves intercepted more light, but the electrons used for net fixation (\( \sum_{e-(CO_2)} \)) were generally unchanged, except for C...
Fig. 7. Light response of fluorescence and constitutive thermal dissipation, $J_{r,D}$ ($y=ax+b$) recorded in ST-I (A), ST-II (B), ST-III (C), and PHV (D); The calculated $r^2$ was 0.98 in ST-I, II, III, and 0.95 in PHV. Each point represents the average of six leaves.

Fig. 8. Light response of light dependent thermal dissipation of inactive PSII and promoted by xanthophyll cycle, $J_{NPQ}$ ($y=a/(b+\ln(1+exp[b(x-c)]))$) recorded in ST-I (A), ST-II (B), ST-III (C), and PHV (D); The calculated $r^2$ was 0.99 in all investigated stages. Each point represents the average of six leaves.
Fig. 9. Light response of photochemical electron transports exiting from PSII (closed squares), $J_{PSII} (y=a(1-\exp(-kx)))$; for non-net carboxylative transports (open triangles), $J_{NC} (y=a(1-\exp(-kx)))$; and effective electron transport for net photosynthesis (closed circles), $J_{CO2} (y=y_0+ax/(b+x))$ recorded in ST-I (A), ST-II (B), ST-III (C), and PHV (D). The $r^2$ in ST-I, II, III, and PHV was 0.97, 0.99, 0.97, and 0.96 for the $J_{PSII}$/irradiance relation, 0.90, 0.97, 0.99, and 0.92 for the $J_{NC}$/irradiance curve and 0.79, 0.95, 0.85, and 0.81 for the $J_{CO2}$/irradiance relation. Each point represents the average of six leaves.

Fig. 10. Light response of electron transport rate for dark respiration and photorespiration ($J_R$, closed squares), and alternative transports ($J_{AT}$, open circles) recorded in ST-I (A), ST-II (B), ST-III (C), and PHV (D). Each point represents the average of six leaves.
samples at post-harvest, where $\sum_{-(CO_2)}$ was statistically lower than for E. Fluorescence and constitutive thermal dissipation ($\Sigma_{e-(fD)}$), but above all non-photochemical quenching ($\Sigma_{e-(NPQ)}$), dissipated more energy in W samples, followed by E and C, respectively. Regardless of light interception, a similar energy amount was funnelled to the non-net carboxylative transports (Table 1).

**Discussion**

**Whole trees**

Canopy inclination and row orientation was varied to create three environments (under natural field conditions) which differed in the intensity and time of the day of peak light interception.

Daily patterns for gas exchange parameters were similar in ST-III and at post-harvest. In the morning, in spite of the differences in light interception recorded at this time, NCU and transpiration were similar among treatments. Available light did not limit net photosynthesis and, thanks to the favourable water and temperature status of the early daytime, stomatal conductance was not limiting in all treatments (Glenn et al., 1999; Jifon and Syvertsen, 2003). At noon, while W light interception was still the highest, NCU and TRWP started to decrease, suggesting a stomatal limitation rather than an influence of light (Fig. 3). In the afternoon, W light interception decreased while the opposite trend was followed by E and C plants. However, W canopies intercepted more light than E and C plants until 14.30 h (Fig. 2). Despite the lower light interception, E canopies showed a further NCU increase till 14.00 h, while net assimilation continued to decrease in C and W trees. As the evapotranspiration demand probably increased in the afternoon, plants responded with stomatal closure, which was followed by a reduction in photosynthesis (Fig. 3). The high irradiance experienced through most of the day by W trees possibly led to canopy temperature increases and to increases in the strictly related vapour pressure deficit (VPD). Stomatal closure can reduce water loss and net photosynthesis (Burrows and Milthorpe, 1976; Farquhar and Sharkey, 1982; Schulze, 1986). Compared to W plants, the E canopy inclination, via lower morning light interception, probably maintained canopy temperature to lower levels for longer during the day. Although VPD increased until 14.00 h, it did not seem to achieve values causing a reduction in stomatal conductance and NCU; as a result, the increased evapotranspiration demand could be met by increased transpiration, while the non-limiting light interception maintained NCU at higher values (Fig. 3). A similar behaviour was observed in apple by Glenn et al. (2003), who applied a highly reflective white particle film to tree canopies, reducing leaf temperature and stomatal limitation and increasing whole plant net assimilation.

In the afternoon, C transpiration increased until 14.00 h while NCU continued to decrease. Afterwards, stomatal closure became limiting even for transpiration and TRWP started to decrease (Fig. 3). This stomatal closure was probably caused by the increasing evapotranspiration demand combined with the low light interception (Jarvis, 1976; Nobel, 2005b). After 15.00 h E water status and VPD probably became limiting, causing a decrease in stomatal conductance to reduce water loss and NCU as well, regardless of the irradiance increase (Fig. 3). Because higher photosynthetic levels were maintained in E plants, although they did transpire more water on a daily basis, their WUE was similar to the other treatments (Fig. 3).

Adding lincomycin to inhibit PSII recovery in leaf discs allowed us to observe the photoinactivation of PSII without the complication of concurrent repair. Assuming the same quantum yield of photoinactivation of PSII applied in conditions that permitted repair, the actual cumulative gross amount of photoinactivated PSII occurring during the day can be calculated from the daily photon exposure. W canopies, which intercepted the most light, showed the lowest daily CO2 assimilation and the highest cumulative gross amount of damaged PSII: about 50% of the total PSII population in peach (Fig. 4). E plants had the highest photosynthetic performance and damage was 8% less than W. The lowest photon exposure was recorded in C plants with 29% lower PSII damage than W but similar daily CO2 uptake (Fig. 4). However, this is an underestimation of the PSII damage occurring in the field as the Qy used was calculated at optimal and steady temperatures.

Table 1. Integrated (between 09.00 h and 17.00 h) mean values for incident irradiance ($\Sigma_{PPFD}$), absorbed energy used for net fixation ($\sum_{-(CO_2)}$) and dissipated via the fluorescence and constitutive thermal dissipation ($\Sigma_{e-(fD)}$), the non-photochemical quenching ($\Sigma_{e-(NPQ)}$) and the non-net carboxylative transports ($\Sigma_{e-(NC)}$) measured four times per day during fruit cell expansion (ST-III) and post-harvest (PHV). Each value is the average of 12 leaves per treatment (six per each side of the canopy) ± SE and was calculated by integration over time.

| Stage | Trt | $\Sigma_{PPFD}$ (mol photons m$^{-2}$) | $\sum_{-(CO_2)}$ (mol e m$^{-2}$) | $\Sigma_{e-(fD)}$ (mol e m$^{-2}$) | $\Sigma_{e-(NPQ)}$ (mol e m$^{-2}$) | $\Sigma_{e-(NC)}$ (mol e m$^{-2}$) |
|-------|-----|--------------------------------------|----------------------------------|-------------------------------|-----------------------------------|---------------------------------|
| ST-III | C   | 24.04±0.01                           | 0.96±0.14                        | 2.34±0.15                     | 4.79±0.15                        | 2.13±0.10                       |
|       | E   | 26.58±0.02                           | 1.07±0.08                        | 2.57±0.12                     | 5.42±0.19                        | 2.24±0.02                       |
|       | W   | 28.81±0.01                           | 0.89±0.11                        | 2.84±0.24                     | 6.29±0.19                        | 2.22±0.12                       |
| PHV   | C   | 21.18±0.02                           | 0.81±0.11                        | 2.07±0.03                     | 3.95±0.14                        | 2.17±0.11                       |
|       | E   | 25.47±0.01                           | 1.02±0.06                        | 2.34±0.24                     | 5.33±0.32                        | 2.14±0.13                       |
|       | W   | 27.82±0.01                           | 0.90±0.08                        | 2.62±0.19                     | 6.03±0.25                        | 2.27±0.20                       |
Single leaves

As the whole canopy data pointed out differences in light management between treatments, single leaf measurements were performed within a range of natural (provided by the asymmetric orchard) irradiance of 150–2100 μmol photons m\(^{-2}\) s\(^{-1}\).

The multivariate principal component analysis showed that all electron transport rates (J) were directly related to irradiance, as should be expected since they serve the purpose of dissipating the incoming energy (Fig. 5). Stomatal conductance (g\(_s\)), air (T\(_{air}\)) and leaf (T\(_{ill}\)) temperature, and vapour pressure deficit (VPD) were correlated with Factor 2, the former positively and the remaining parameters negatively. VPD is directly proportional to saturating vapour pressure and therefore to temperature; arguably, leaves coped with water loss by reducing stomatal conductance (Gindaba and Wand, 2007). The PCA analysis clearly showed that J\(_{CO_2}\) and J\(_{AT}\) were the most related to stomatal conductance and temperature among all the J parameters (Fig. 5), as shown by their correlation to the second principal component (Farquhar et al., 1980).

The energy fraction (Q\(_{TD}\)) dissipated by the combined fluorescence and constitutive thermal dissipation was constant at all irradiances as shown by the linear relation of J\(_{TD}\) with irradiance (Fig. 7). This almost constant thermal and fluorescence dissipation is the consequence of the exciton–radical pair equilibrium and the relatively slow electron transfer from pheophytin\(^-\) to the primary quinone acceptor, compared with charge recombination to the excited state (Hendrickson et al., 2004). Non-net carboxylative transports (J\(_{NC}\)) increased linearly with irradiance until 1000–1200 μmol photons m\(^{-2}\) s\(^{-1}\), following, probably, an enzymatic first-order relation (Fig. 9). The enzymes involved in the cycles were fully activated and, as more electrons were moved by light, more electrons were dissipated via photochemistry. Above 1000–1200 μmol photons m\(^{-2}\) s\(^{-1}\) J\(_{NC}\) did not increase because the regeneration of electron carriers was probably limiting (Foyer and Harbinson, 1994). Even though non-net carboxylative transports are generally more dangerous than NPQ because of increased ROS formation during the intermediate steps, these mechanisms were first activated while J\(_{NPQ}\) responded to a limited extent to the medium-low irradiances (Fig. 8). The main mechanism involved in thermal dissipation is the strictly trans-thylakoid ΔpH-dependent xanthophyll cycle and the optimum lumen pH for violaxanthin de-epoxidase activity is under 6.5 (Bratt et al., 1995). Probably, at medium-low irradiance, the thylakoid lumen was not sufficiently acidic to activate VDE completely. Leaves thus might have been able to dissipate the excess energy by alternative ways (Figs 8, 9). It is noteworthy that the water–water cycle, the cyclic transport around PSI, and the glutathione–ascorbate cycle are all able to increase the trans-thylakoid ΔpH, contributing to creating the optimal pH environment for VDE (Heber and Walker, 1992; Noctor and Foyer, 1998; Asada, 1999; Cruz et al., 2005). Above 800–1000 μmol photons m\(^{-2}\) s\(^{-1}\), lumen pH was probably optimal for VDE activation and J\(_{NPQ}\) started to increase linearly.

At all irradiance levels, and particularly above the photosynthetic saturation point, J\(_{CO_2}\) could not handle all the incoming energy, the excess of which had to be quenched by the other energy users, first of all non-photochemical quenching (Figs 8–9). Although a trend was generally apparent, a considerable scatter was nonetheless recorded (Fig. 9A, C, D), probably because, as shown in the PCA analysis, net photosynthesis was also related to temperature and stomatal conductance, in addition to irradiance (Farquhar et al., 1980). J\(_P\) increased proportionally with irradiance never reaching a saturating point (Fig. 10). Although photorespiration consumes CO\(_2\) it might be a necessary loss to deal with excess light or other environmental stresses (Osmond, 1981; Flexas et al., 2002; Galmés et al., 2007). The estimation of J\(_{AT}\) performed here is affected by leaf temperature, conductance, net photosynthesis (see PCA analysis), compensation point, and dark respiration, which in turn are easily influenced by the environment. This makes J\(_{AT}\) difficult to estimate (von Caemmerer, 2000) and probably explains why a clear pattern against irradiance was never found (Fig. 10).

The strong dependence of energy dissipation on non-photochemical quenching was further highlighted by the integration of the irradiance and the J parameters data collected at the leaf level (Table 1). In accordance with whole canopy observations, the higher amount of photons intercepted by W leaves did not promote an increase in carbon assimilation. On the contrary, excessive light was mainly dissipated by the ΔpH-dependent non-photochemical quenching. The contribution of the non-net carboxylative transports for energy quenching seemed to already achieve its steady-state in C leaves that had intercepted the lowest amount of photons (Table 1).

Conclusions

The ‘asymmetric’ peach orchard demonstrates that row orientation and canopy inclination can be used to provide, under natural conditions, quite diverse daily light interception profiles which allow the relationship among the absorbed light energy, photosynthetic performance, protective strategies, and water use in the field to be studied.

Net carboxylation increased with irradiance until reaching a saturation point. Excess light that cannot enhance photosynthesis may impose water and thermal stresses, leading to the stomatal limitation of gas exchanges. Intercepting less light, C plants showed the lowest photo-inhibition but equalled W in CO\(_2\) uptake and water use. E trees assimilated more CO\(_2\) and transpired more water than C and W, exhibiting an intermediate extent of PSII damage. The highest extent of cumulative gross photoactivation of PSII was found in W trees in which the higher total light interception did not promote net carboxylation but proved to be in excess, exacerbating PSII damage. Since damaged photosystems are quickly repaired at the expense of energy (Chow and Aro, 2005; Nixon et al., 2005), it would be important to investigate the cost of PSII recovery in terms of diminished whole-plant and/or fruit productivity.
The management of absorbed energy may be modulated by irradiance. At medium–low irradiance $NPQ$ appeared limited, probably by a low $trans$-thylakoidal $\Delta pH$, while net photosynthesis and the non-net carboxylative transports increased linearly with irradiance, reaching a steady state. These alternative pathways were the principal quenching mechanisms under low light and are probably used for creating the optimal $trans$-thylakoidal $\Delta pH$ for violaxanthin de-epoxidase functioning as well. At over-saturating light, when the xanthophyll cycle was fully activated, $NPQ$ became the main dissipation pathway, probably supported by photorespiration.

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Appendix
List of abbreviations

C Chloroplast CO$_2$ concentration ($\mu$bar)  
$C_i$ Intercellular CO$_2$ concentration ($\mu$bar)  
$F_m$ Maximum chlorophyll fluorescence for a dark-adapted leaf  
$F'_m$ Maximum chlorophyll fluorescence for a light-adapted leaf  
$F_o$ Minimum chlorophyll fluorescence for a dark-adapted leaf  
$F_s$ Steady-state fluorescence  
$F_v$ Variable fluorescence ($F_m - F_o$)  
$F_v/F_m$ Maximum quantum yield of photosystem II (0–1, dimensionless)  
$g_l$ Internal diffusion conductance (mol m$^{-2}$ s$^{-1}$)  
$g_s$ Stomatal conductance (mol m$^{-2}$ s$^{-1}$)  
$J_A$ Electrons used for photosynthesis and photorespiration (mol m$^{-2}$ s$^{-1}$)  
$J_{AT}$ Electrons used for the alternative transports (mol m$^{-2}$ s$^{-1}$)  
$J_{CO_2}$ Net photosynthesis expressed as electron transport rate (mol m$^{-2}$ s$^{-1}$)  
$J_{LD}$ Energy amount dissipated via the fluorescence and constitutive thermal dissipation, expressed as electron transport rate (mol m$^{-2}$ s$^{-1}$)  
$J_{NC}$ Electrons used for the non-net carboxylative transports (mol m$^{-2}$ s$^{-1}$)  
$J_{NPQ}$ Energy amount dissipated via the light dependent non-photochemical quenching, expressed as electron transport rate (mol m$^{-2}$ s$^{-1}$)  
$J_{PSII}$ Electrons exiting from PSII (mol m$^{-2}$ s$^{-1}$)  
$J_{R}$ Electrons used for mitochondrial respiration and photorespiration (mol m$^{-2}$ s$^{-1}$)  
$J_{TOT}$ Absorbed irradiance expressed as electron transport rate (mol m$^{-2}$ s$^{-1}$)  
$NCU$ Whole canopy net CO$_2$ carbon uptake (mol m$^{-2}$ s$^{-1}$)  
$P_n$ Rate of net photosynthesis (mol m$^{-2}$ s$^{-1}$)  
$PPFD$ Irradiance (mol m$^{-2}$ s$^{-1}$)  
$Q_y$ Quantum yield of photoinactivation (mol PSII mol$^{-1}$ photons)  
$R_d$ Dark respiration (mol m$^{-2}$ s$^{-1}$)  
$T_{air}$ Air temperature ($^\circ$C)  
$T_{lf}$ Leaf temperature ($^\circ$C)  
$Tr$ Transpiration (mmol m$^{-2}$ h$^{-1}$)  
$TR_{WP}$ Whole canopy specific water transpiration (l m$^{-2}$ h$^{-1}$)  
$VPD$ Vapour pressure deficit (kPa)  
$WUE$ Water use efficiency (mol l$^{-1}$)  
$\Gamma*$ Compensation point in the absence of mitochondrial respiration ($\mu$bar)  
$\Sigma_{-CO_2}$ Mean integrated absorbed energy used for net fixation (mol e$^-\cdot$m$^{-2}$)  
$\Sigma_{(f;D)}$ Mean integrated absorbed energy dissipated via the fluorescence and constitutive thermal dissipation (mol e$^-\cdot$m$^{-2}$)  
$\Sigma_{(NC)}$ Mean integrated absorbed energy dissipated via the non net carboxylative transports (mol e$^-\cdot$m$^{-2}$)  
$\Sigma_{NPQ}$ Mean integrated absorbed energy dissipated via the non-photochemical quenching (mol e$^-\cdot$m$^{-2}$)  
$\Sigma_{PPFD}$ Mean integrated incident irradiance (mol m$^{-2}$)  
$\Phi_{LD}$ Quantum efficiency of fluorescence and constitutive thermal dissipation (0–1, dimensionless)  
$\Phi_{NPQ}$ Quantum efficiency of the light-dependent non-photochemical quenching (0–1, dimensionless)  
$\Phi_{PSII}$ Quantum efficiency of photochemical processes (0–1, dimensionless)

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