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Effects of Kaolin Application on Light Absorption and Distribution, Radiation Use Efficiency and Photosynthesis of Almond and Walnut Canopies

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• *Background and Aims* Kaolin applied as a suspension to plant canopies forms a film on leaves that increases reflection and reduces absorption of light. Photosynthesis of individual leaves is decreased while the photosynthesis of the whole canopy remains unaffected or even increases. This may result from a better distribution of light within the canopy following kaolin application, but this explanation has not been tested. The objective of this work was to study the effects of kaolin application on light distribution and absorption within tree canopies and, ultimately, on canopy photosynthesis and radiation use efficiency.
• *Methods* Photosynthetically active radiation (PAR) incident on individual leaves within the canopy of almond (*Prunus dulcis*) and walnut (*Juglans regia*) trees was measured before and after kaolin application in order to study PAR distribution within the canopy. The PAR incident on, and reflected and transmitted by, the canopy was measured on the same day for kaolin-sprayed and control trees in order to calculate canopy PAR absorption. These data were then used to model canopy photosynthesis and radiation use efficiency by a simple method proposed in previous work, based on the photosynthetic response to incident PAR of a top-canopy leaf.
• *Key Results* Kaolin increased incident PAR on surfaces of inner-canopy leaves, although there was an estimated 20 % loss in PAR reaching the photosynthetic apparatus, due to increased reflection. Assuming a 20 % loss of PAR, modelled photosynthesis and photosynthetic radiation use efficiency (PRUE) of kaolin-coated leaves decreased by only 6·3 %. This was due to (1) more beneficial PAR distribution within the kaolin-sprayed canopy, and (2) with decreasing PAR, leaf photosynthesis decreases less than proportionally, due to the curvature of the photosynthesis response-curve to PAR. The relatively small loss in canopy PRUE (per unit of incident PAR), coupled with the increased incident PAR on the leaf surface on inner-canopy leaves, resulted in an estimated increase in modelled photosynthesis of the canopy (+9 % in both walnut and almond). The small loss in PRUE (per unit of incident PAR) resulted in an increase in radiation use efficiency per unit of absorbed PAR, which more than compensated for the minor (7 %) reduction in canopy PAR absorption.
• *Conclusions* The results explain the apparently contradictory findings in the literature of positive or no effects of kaolin applications on canopy photosynthesis and yield, despite the decrease in photosynthesis by individual leaves when measured at the same PAR.

Key words: *Juglans regia*, kaolin particle film, modelling, photosynthesis, *Prunus dulcis*, radiation use efficiency.

INTRODUCTION

Particle film technology (i.e. spraying canopies with a suspension of particles of various kinds of clay, leaving a film on the leaves) has long been used to limit the impact of water and heat stress on crops. Possible mechanisms for these effects were discussed in a previous paper (Rosati *et al.*, 2006). Earlier work, focused primarily on crop yield, has suggested that particle film applications, in some crops and under some conditions, increases yield, for example in sorghum (Stanhill *et al.*, 1976), cotton (Moreshet *et al.*, 1979), tomato (Srinivasa Rao, 1985), peanut (Soundara Rajan *et al.*, 1981) and apple (Glenn *et al.*, 2001). More recent and detailed work, carried out using a kaolin particle film (Surround WP, Engelhard, Iselin, NJ), suggests that it generally reduces photosynthetic rates of individual leaves (Grange *et al.*, 2004; Wünsche *et al.*, 2004) except under high temperature and/or heat stress (Glenn *et al.*, 2003; Jifon and Syvertsen, 2003). The decrease in leaf photosynthesis is related to the reduction in light reaching the photosynthetic apparatus, due to a 20–40 % increase in reflection and decreased absorption (Abou-Khaled *et al.*, 1970; Moreshet *et al.*, 1979; Wünsche *et al.*, 2004; Rosati *et al.*, 2006). The effects of kaolin application on canopy photosynthesis have rarely been measured. Wünsche *et al.* (2004) found that it did not decrease canopy photosynthesis despite a reduction in photosynthetic rates of individual leaves; indeed, Glenn *et al.* (2003) found an increase in canopy photosynthesis. These data agree with unaffected or increased yields with kaolin application, respectively. What remains unclear is why decreased leaf photosynthesis does not decreased canopy photosynthesis. Wünsche *et al.* (2004) suggested that this is due to improved light distribution within the canopy, but no studies have tested this hypothesis.

The relationship between individual-leaf and canopy photosynthesis can be explored by means of modelling.

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The advantage of this approach is that a model can be used to test hypotheses and explain possible mechanisms, whilst measurement of canopy photosynthesis alone does not explain why an increase or decrease might occur.

In previous work (Rosati and DeJong, 2003; Rosati *et al.*, 2004) we proposed a simple method to estimate the photosynthetic radiation use efficiency (PRUE) and photosynthesis of canopies. It is assumed that all leaves in a canopy have the same PRUE when photosynthesis and radiation are integrated over a day. Thus, a hypothetical leaf at the top of the canopy, exposed to above-canopy incident radiation (which can be obtained from a weather station) has the same PRUE as all other leaves and therefore can be used to estimate canopy PRUE. This simple method may prove useful to estimate the effect of kaolin applications on canopy PRUE and photosynthesis, provided that the treatment does not undermine the assumption that PRUE is constant among leaves throughout the canopy.

The first objective of this study was to measure the effect of kaolin application on PAR absorption by the canopy and on PAR distribution on individual leaves within the canopy. The second objective was to verify whether the assumption that PRUE is constant throughout the canopy, as well as for the hypothetical leaf, remains valid with kaolin application. This would allow the simple method to be used. The third objective was to use the simple method (if the second objective was achieved) to estimate the effect of kaolin application on canopy PRUE and photosynthesis.

To test the interaction between kaolin application and canopy type, kaolin was sprayed on trees of species with contrasting leaf size and canopy density, namely almond (*Prunus dulcis*) and walnut (*Juglans regia*).

MATERIALS AND METHODS

Plant material and growing conditions

The experiment was carried out during the summer of 2003 on an 8-year-old almond [*Prunus dulcis* (Mill) D.A. Webb, 'Nonpareil'] orchard in Solano county (38°28′41″N, 121°51′31″W), California, and a 10-year-old walnut (*Juglans regia* L. 'Chandler') orchard in Tehama county (39°53′11″N, 122°18′59″W), California. Tree spacing was 6 × 7 m for almond and 4·7 × 7·3 m for walnut. Almonds were trained to an 'open vase' and were about 5·5 m tall and 5 m wide, while walnuts were trained to a hedgerow configuration, hedged on alternate sides each year, and were about 10·5 m tall by 7 m wide. The crops received routine horticultural care suitable for commercial production including fertilization, irrigation, weed and pest control.

The walnut orchard was irrigated every 2–3 d with micro-sprinklers, providing water to about 100 % crop evapotranspiration (ETc). The almond orchard was irrigated every other week with about 100 % ETc. The ETc was calculated weekly, based on an estimated crop coefficient (Goldhamer and Snyder, 1989) and modified Penman reference crop water-use (ET_0) obtained from CIMIS (California Irrigation Management Information System, CA, USA) weather stations nearest to each site (<10 km for almond and 35 km for walnut).

On 17 July for almond and on 18 August for walnut, on two areas of each orchard, a 6 % suspension of kaolin (Surround WP, Engelhard, Iselin, NJ) in water, with no adhesive or other compounds, was sprayed (with a John Bean model 1010 sprayer, Durand-Wayland, Inc., LeGrange GA, for almond and a Rear's engine-driven pull-tank sprayer, Rear's Manufacturing Company, Eugene, OR, for walnut) from above the canopies to run-off on the foliage. Each sprayed area comprised three rows by four trees (total of 12 trees), and the two areas were about 100 m apart in the walnut orchard and 50 m apart in the almond orchard. Two control areas of 12 trees were chosen in each orchard near the kaolin-treated areas, but leaving one row of trees as a border. The kaolin treatment resulted in a relatively uniform coating of kaolin film on leaves as evaluated visually, at least on the outer-canopy, but this uniformity was not measured.

Canopy light absorption

The day after kaolin application, the PAR reflected from and transmitted by the canopy was measured using a ceptometer light bar (Decagon Devices, Pullman, WA). For each species (i.e. almond and walnut) and for each treatment (i.e. kaolin and control) six rectangular areas (three in each 12-tree area), having four adjacent tree trunks as corners, were selected avoiding border effects. For the reflected PAR, the light bar was held with the sensors orientated downwards about 2 m above the highest part of the canopy; for the transmitted PAR, the light bar was held at ground level, with the sensor orientated upwards. About 100 measurements were taken in each area whilst the light bar was moved to cover the whole area. The 100 readings were then averaged automatically and this value was recorded. Measurements were repeated, on the same areas, five times during the day for walnut and seven times for almond. The data were then integrated over the day and were used to calculate the fractions of the daily PAR incident above the canopy (R_{inc}) that were either transmitted ($R_{\mathrm{tr,C}}$ and $R_{\mathrm{tr,K}}$ for control and kaolin treatments, respectively) or reflected ($R_{\mathrm{ref,C}}$ and $R_{\mathrm{tr,K}}$ for control and kaolin, respectively). R_{inc} was obtained from the CIMIS weather stations. CIMIS data (hourly averages) for incident global radiation (GR, watts m^{-2} h^{-1}) were converted into PAR (mol m^{-2} h^{-1}) based on a regression between GR and PAR as measured by a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE). The regression was as follows: $\mathrm{PAR} = 1{\cdot}9875 + 0{\cdot}1593\mathrm{GR}$, $R^2 = 0{\cdot}98$. Canopy PAR absorption for the control ($R_{\mathrm{abs,C}}$) and the kaolin ($R_{\mathrm{abs,K}}$) treatments were then calculated as:

$$R_{\mathrm{abs,C}} = R_{\mathrm{inc}}(1 - R_{\mathrm{tr,C}} - R_{\mathrm{ref,C}}) \tag{1}$$

$$R_{\mathrm{abs,K}} = R_{\mathrm{inc}}(1 - R_{\mathrm{tr,K}} - R_{\mathrm{ref,K}}) \tag{2}$$

Canopy light distribution

The PAR incident on individual leaves was measured (Rosati *et al.*, 2004) using two sets of sensors, each with 50 lightweight (0·1 g) GaAsP photosensors (Hamamatsu, Japan), individually calibrated with a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE) and connected to two dataloggers (DL2e, Delta-T Devices Ltd, Cambridge, UK). The sensors were placed on the adaxial surface of 50 leaves throughout the canopy of a selected tree (two trees selected, one for each 50-sensor set). The PAR incident on each leaf was measured every 60 s from 0500 to 2100 h, the day before and the day after kaolin application without moving the sensors. The two days were clear and had similar incident PAR, totalling about 58 and 56 mol m^{-2} d^{-1} for almond and 52 and 49 mol m^{-2} d^{-1} for walnut before and after kaolin application, respectively. To avoid applying kaolin on the photosensors, they were carefully covered with tape before spraying and, upon drying of the kaolin film, the tape was removed. Data from sensors that had moved from the original position were discarded.

To determine the effect of kaolin application on light distribution within the canopy, the daily PAR incident on each sampled leaf after spraying was compared with that incident on the same leaf before spraying. Since incident PAR changed, albeit minimally, between the day before and the day after kaolin application, the comparison was made by expressing the PAR incident on individual leaves as a fraction of the total incident PAR of the same day.

Based on the literature (Wünsche *et al.*, 2004), we assumed that the PAR actually reaching the photosynthetic system in kaolin-coated leaves was 80 % of that incident on them (i.e. the PAR measured by the sensors) and compared this estimated PAR with that incident on the leaves before kaolin application.

Modelling canopy PRUE and photosynthesis

The daily photosynthetic radiation use efficiency (PRUE, abbreviated as E in our equations; see Appendix) and net photosynthesis of the canopy (daily A_n) were estimated as described by Rosati *et al*, (2004; note that A_n refers to the *canopy* throughout the following text). In summary, the light data collected for the 50 sampled leaves per tree were coupled with the photosynthetic response curves to PAR of those leaves (as estimated from their light-saturated photosynthesis, which was measured for all leaves between 0900 and 1400 h on the same day, but before kaolin application) to estimate the daily net photosynthesis of each leaf. This was plotted against the daily PAR incident on the leaf to derive the PRUE (i.e. slope of the regression) of all leaves and thus of the canopy. In addition, the PRUE of leaves and canopy was also estimated by plotting the daily photosynthesis against the daily PAR incident on a hypothetical leaf at the top of the canopy (i.e. the incident PAR, R_{inc}, obtained from the weather station), having the photosynthetic properties of a top-canopy leaf. The PRUE calculated with the 50-leaf model is termed $E_{50\mathrm{L}}$, whilst that calculated from the hypothetical leaf model is termed E_{HL} (see Appendix for all abbreviations used in equations).

To calculate $E_{50\mathrm{L}}$ and E_{HL} with kaolin application, we assumed that the kaolin film reduced the PAR available for the leaves to 80 % of that incident (Wünsche *et al.*, 2004), as measured by the sensors for the 50-leaf model or by the weather station for the hypothetical leaf, and ran both models with the corrected PAR data. This reduced daily photosynthesis and thus PRUE (per unit of PAR incident), the latter being termed $E_{50\mathrm{L,R80}}$ and $E_{\mathrm{HL,R80}}$ for the 50-leaf and the hypothetical-leaf models, respectively.

To determine the effect of kaolin application on canopy PRUE, we compared $E_{50\mathrm{L,R80}}$ and $E_{\mathrm{HL,R80}}$ (i.e. model runs with 80 % of measured incident PAR) with $E_{50\mathrm{L,R100}}$ and $E_{\mathrm{HL,R100}}$, respectively (i.e. model runs for the same day, but with 100 % of measured incident PAR).

If the simple method of Rosati and DeJong (2003) and Rosati *et al.* (2004) worked under kaolin application, then we could estimate daily net photosynthesis of the canopy with kaolin application ($A_{\mathrm{n,K}}$) or without (control, $A_{\mathrm{n,C}}$), for the same day, as:

$$A_{\mathrm{n,C}} = \frac{(R_{\mathrm{abs,C}})(E_{\mathrm{HL,R100}})}{(S_{\mathrm{leaf,C}})} \qquad (3)$$

and

$$A_{\mathrm{n,K}} = \frac{(R_{\mathrm{abs,K}})(E_{\mathrm{HL,R80}})}{(S_{\mathrm{leaf,K}})} \qquad (4)$$

where $S_{\mathrm{leaf,C}}$ and $S_{\mathrm{leaf,K}}$ are the leaf PAR absorption for control and kaolin treatments, respectively. $S_{\mathrm{leaf,C}}$ was assumed to be constant throughout the canopy and, by definition, $S_{\mathrm{leaf,K}} = 0{\cdot}8 S_{\mathrm{leaf,C}}$ (i.e. 80 %).

RESULTS AND DISCUSSION

Effect of kaolin application on canopy light absorption

In both species, kaolin application increased the PAR reflected whilst having no effect on PAR transmission (Fig. 1). Integrated over the day and expressed as a fraction of daily incident PAR (R_{inc}), canopy reflection increased by about $0{\cdot}06R_{\mathrm{inc}}$ (from 0·03 in the control areas to 0·09 in the kaolin-sprayed areas) in walnut, and by about $0{\cdot}05R_{\mathrm{inc}}$ (from 0·04 to 0·09) in almond. Daily integrated transmitted PAR was not affected by kaolin and was $0{\cdot}15R_{\mathrm{inc}}$ in walnut and about $0{\cdot}29R_{\mathrm{inc}}$ in almond. Using eqns (1) and (2), absorption values were obtained for walnut:

$$R_{\mathrm{abs,C}} = R_{\mathrm{inc}}(1 - 0{\cdot}15 - 0{\cdot}03) = 0{\cdot}82R_{\mathrm{inc}} \qquad (5)$$

$$R_{\mathrm{abs,K}} = R_{\mathrm{inc}}(1 - 0{\cdot}15 - 0{\cdot}09) = 0{\cdot}76R_{\mathrm{inc}} \qquad (6)$$

and for almond:

$$R_{\mathrm{abs,C}} = R_{\mathrm{inc}}(1 - 0{\cdot}29 - 0{\cdot}04) = 0{\cdot}67R_{\mathrm{inc}} \qquad (7)$$

$$R_{\mathrm{abs,K}} = R_{\mathrm{inc}}(1 - 0{\cdot}29 - 0{\cdot}09) = 0{\cdot}62R_{\mathrm{inc}} \qquad (8)$$

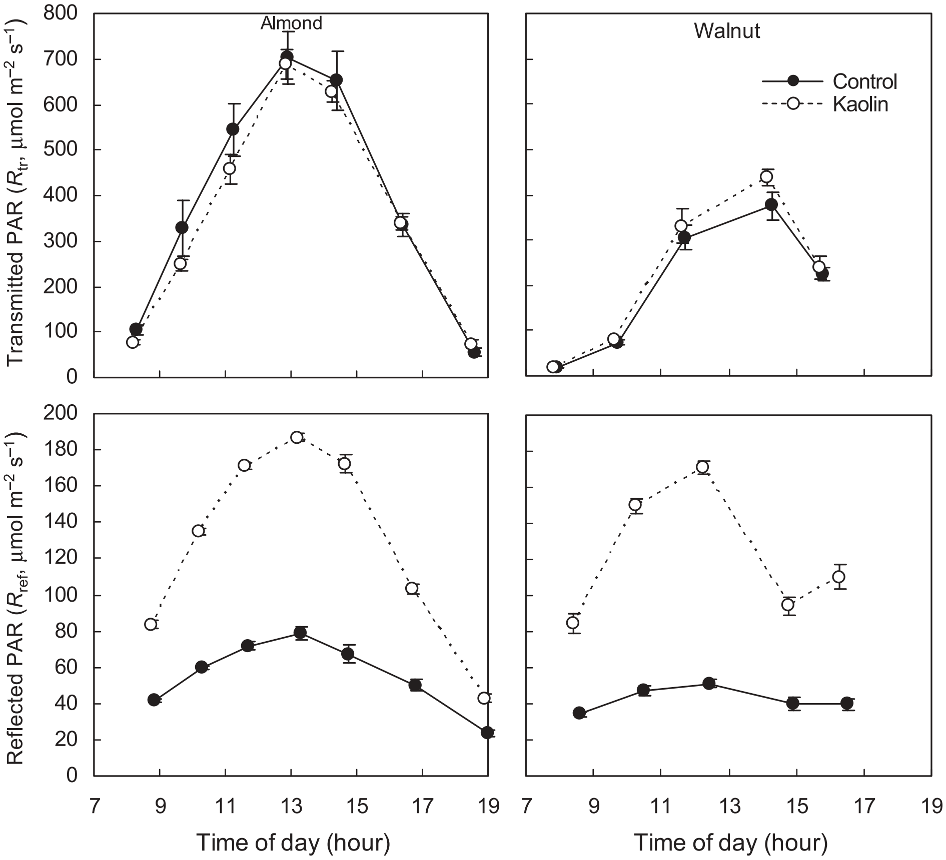

FIG. 1. Daily course of PAR transmitted (R_{tr}) and reflected (R_{ref}) by the canopy in walnut and almond trees for control and kaolin-treated plants. Each point represents the average of six measurements, each of which is the average of 100 individual readings. Bars indicate s.e. (when not visible, bars are smaller than the symbols).

Combining eqns (5) and (6) for walnut:

$$\frac{R_{abs,K}}{R_{abs,C}} = 0{\cdot}93 \tag{9}$$

Combining eqns (7) and (8) for almond:

$$\frac{R_{abs,K}}{R_{abs,C}} = 0{\cdot}93 \tag{10}$$

From eqns (9) and (10) it can be concluded that kaolin reduced canopy light absorption by about 7 % in both species, compared with the untreated controls.

Effect of kaolin application on PAR distribution within the canopy

For a given daily incident PAR above the canopy, kaolin application increased the daily PAR incident on individual inner-canopy leaves, as measured by the photosensors (Fig. 2A, B). In both species, this increase was up to more than 200 % of the PAR incident before kaolin application on some of the inner-canopy leaves (i.e. leaves exposed to lower incident PAR). Most of the photosensors were placed on outer-canopy leaves and only few on inner-canopy leaves (since PAR decreases exponentially with canopy depth and we wanted a uniform distribution of PAR values). However, most of the leaves in the tree are actually inner-canopy leaves, which thus experienced increased incident PAR with kaolin application.

Data in Fig. 2A and B are for the PAR incident on the kaolin-coated leaves as measured by the photosensors, without accounting for the reduction of PAR actually available below the kaolin film. When this reduction was accounted for (i.e. assuming a 20 % reduction), then kaolin application reduced the PAR actually available for most sunlit leaves, while some inner-canopy leaves still received more PAR than without kaolin application (Fig. 2C, D). While we assumed that all leaves were treated uniformly, it is quite possible that inner-canopy leaves received a thinner kaolin coating so that the PAR actually available for these leaves was greater than estimated in Fig. 2C, D.

These results support the hypothesis that kaolin application affects canopy light distribution (Wünsche *et al.*, 2004). Our data show that this distribution is skewed in favour of inner-canopy leaves, which receive greater irradiance than without kaolin applications (Fig. 2 A, B). This is also supported by the fact that kaolin application

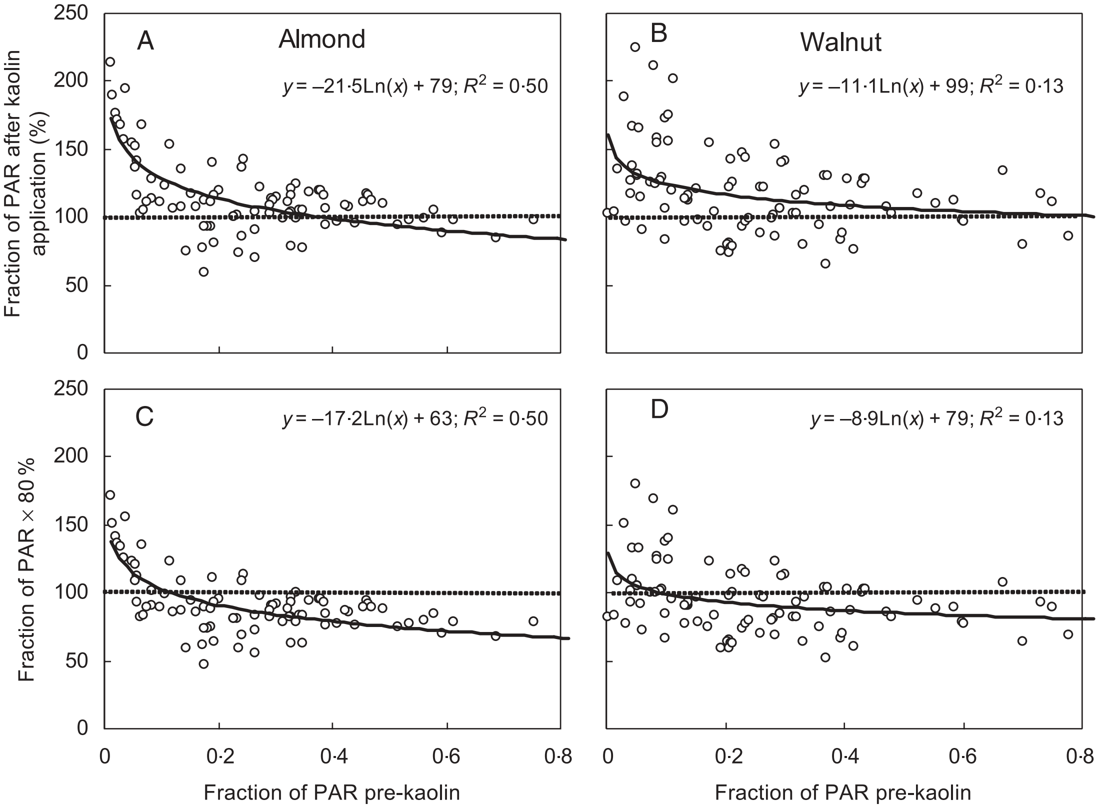

Fig. 2. Fraction of daily incident PAR (i.e. PAR incident on leaves/PAR above canopy) measured by photosensors on individual leaves after kaolin application (A, B), or reduced to 80 % of the photosensors' readings (C, D), expressed as a percentage of the fraction of daily incident PAR on the same leaves before kaolin application. Data above the dotted lines represent leaves where incident PAR increased with kaolin application. The solid lines are fits to the data; regression equations are shown in the graphs.

reduced canopy PAR absorption by only 7 % in both species, despite a 20–40 % loss in leaf absorption (Abou-Khaled *et al.*, 1970; Moreshet *et al.*, 1979; Wünsche *et al.*, 2004; Rosati *et al.*, 2006). This implies that a great part of the additional PAR reflection at the leaf level is re-intercepted and eventually absorbed within the canopy.

Correct use of the simple method to estimate PRUE with kaolin application

Before kaolin was applied, the simple method to estimate PRUE worked, as expected: E_{HL} was within 1 % of E_{50L} and the daily net photosynthesis of individual leaves was linearly related to the daily PAR incident on them (Figs 3A and 4).

When the PAR distribution throughout the canopy as altered by the kaolin application was used to run the models without accounting for the shading effect of kaolin on the individual leaves, the PRUE estimated with the 50-leaf model was 7·5 % greater than that predicted by the simple method (i.e. $E_{\mathrm{50L,R100}} = 1{\cdot}075E_{\mathrm{HL,R100}}$; Figs 3B and 4). This increase was an artefact, since the PAR used in this exercise was that measured by the sensors without correcting for the shading effect of kaolin on the leaf. However, this exercise showed that the PAR distribution as altered by the kaolin application had the effect, *per se*, of increasing canopy PRUE. In fact, since the two models yielded similar values of PRUE before kaolin application, we can assume that $E_{\mathrm{HL,R100}}$ represents the PRUE that the canopy would have had on that day if kaolin had not been applied. Consequently, the 7·5 % increase in PRUE estimated with the 50-leaf model was entirely due to the altered PAR distribution within the canopy caused by kaolin application. The positive effect of the altered PAR distribution on PRUE can be explained by considering that kaolin application decreased the light incident on outer-canopy leaves and increased it on inner-canopy leaves (Fig. 2). In fact, top-canopy leaves often operate near light saturation and their PRUE is improved at lower light, while inner-canopy leaves operate more often at low light and their PRUE is improved at higher light (Hirose and Bazzaz, 1998). Skewing the light distribution towards inner-canopy leaves, as kaolin application did (Fig. 2), would therefore result in improved canopy PRUE, as previously found in *Prunus* under water stress (Lampinen *et al.*, 2004) or as commonly found with diffuse light, which penetrates the canopy better than direct radiation (Spitters, 1986; Sinclair *et al.*, 1992).

When the shading effect of kaolin was considered (i.e. PAR actually available for leaf photosynthesis, equal to 80 % of the PAR incident above the kaolin-coated leaf),

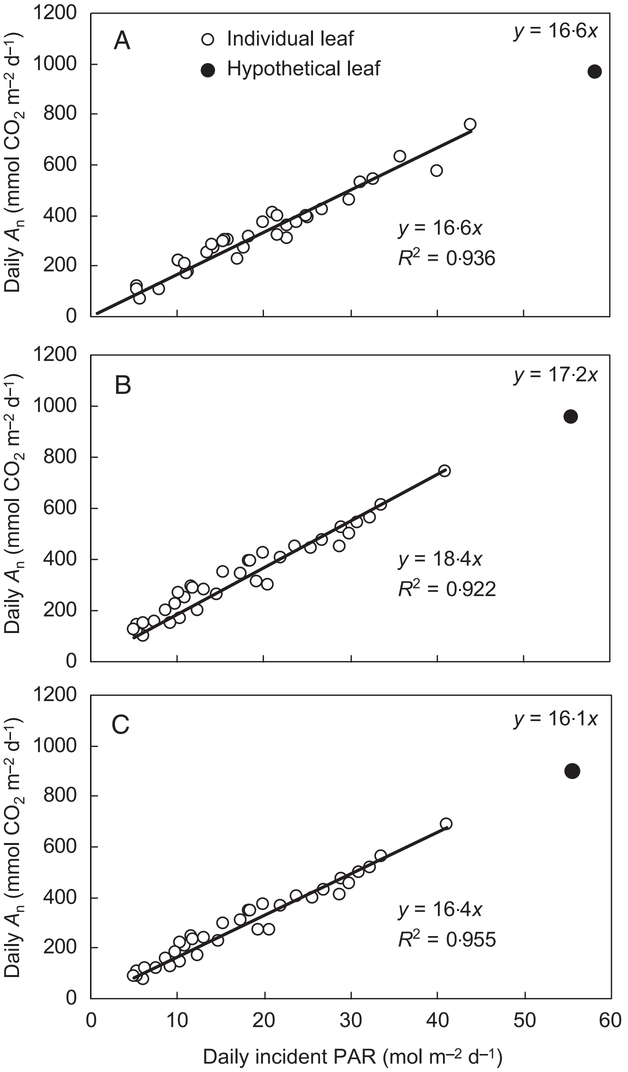

FIG. 3. Relationship between net CO_2 assimilation integrated over a day (daily A_n) and daily incident PAR of individual leaves and for a hypothetical leaf at the top of the canopy. Data are for one almond tree on (A) the day before kaolin application; (B) the day after kaolin application using the PAR data as measured by photosensors (for the 50 leaves) or a weather station (for the hypothetical leaf); and (C) the day after kaolin application using 80 % of the photosensors' or weather station's readings. Comparison between the slopes (PRUE) for the individual leaves and the hypothetical leaf for two almond and two walnut trees are shown in Fig. 4.

then the PRUE estimated with the 50-leaf model (i.e. $E_{50L,R80}$) and that estimated with the hypothetical-leaf model (i.e. $E_{HL,R80}$) were similar (within 1·8 %; Figs 3C and 4) and the 50-leaf data points were still linear (Fig. 3C), thus allowing for the correct use of the simple method to estimate PRUE.

Effect of kaolin application on PRUE

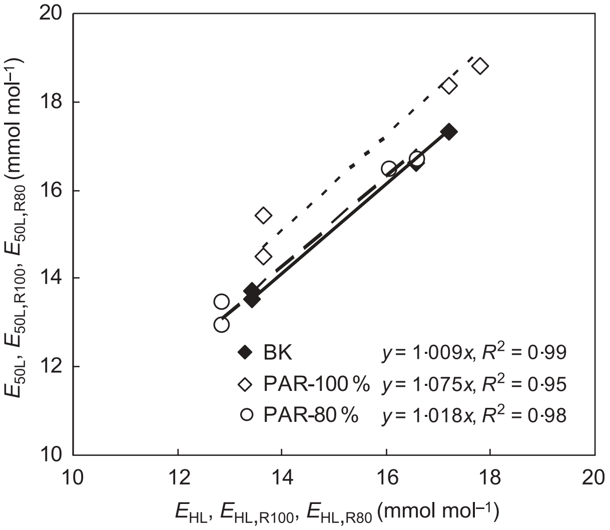

FIG. 4. Relationship between the photosynthetic radiation use efficiency calculated with the 50-leaf model before kaolin application (BK, E_{50L}), after kaolin application with the PAR as measured by the photosensors (PAR-100 %, $E_{50L,R100}$), or reducing PAR to 80 % (PAR-80 %, $E_{50L,R80}$), with the photosynthetic radiation use efficiency calculated with the hypothetical-leaf method before kaolin application (E_{HL}), after kaolin application with the PAR as measured by the weather station ($E_{HL,R100}$), or with PAR reduced to 80 % ($E_{50L,R80}$). Each point represents one tree. Data are for two almond and two walnut trees.

After the simple method predicted PRUE comparably to the 50-leaf model, it was then used to estimate the PRUE of the canopy with and without kaolin application for the same day and the same trees; this was necessary because the PRUE changes from day to day with incident radiation (De Witt, 1965; Norman and Arkebauer, 1991; Sinclair *et al.*, 1992; Hammer and Wright, 1994; Bange *et al.*, 1997). Thus comparing the PRUE from two different days, before and after kaolin application, would not have been correct. The results indicated a 6·3 % reduction of PRUE with kaolin (i.e. $E_{HL,R80} = 0{\cdot}937 E_{HL,R100}$; Fig. 5).

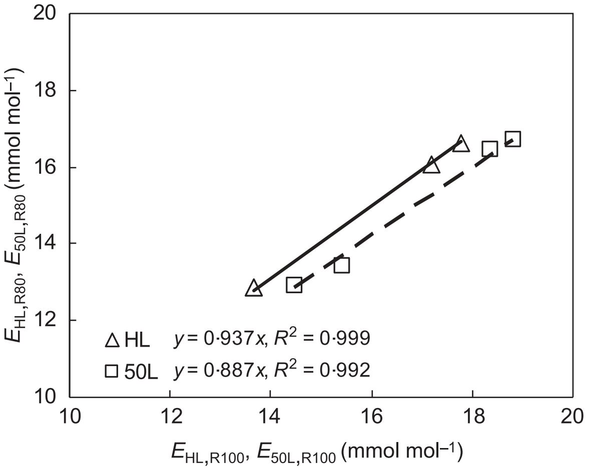

FIG. 5. Relationship between photosynthetic radiation use efficiency calculated after kaolin application with the PAR reduced to 80 % using the 50-leaf model (50L, $E_{50L,R80}$) or the hypothetical-leaf method (HL, $E_{HL,R80}$), with the photosynthetic radiation use efficiency calculated for the same day with the PAR measured by the photosensors or weather station, using the 50-leaf model ($E_{50L,R100}$) or the hypothetical-leaf method ($E_{HL,R100}$).

When the 50-leaf model was used (i.e. $E_{50L,R80}$ compared to $E_{50L,R100}$), the reduction of PRUE with kaolin was greater (11·3 %; Fig. 5). This was an artefact, since $E_{50L,R100}$ was overestimated, as explained above, by not accounting for the shading effect of the kaolin film. However, this exercise showed that a 20 % reduction in PAR incident on leaves resulted, *per se*, in a less than proportional reduction in E_{50L}. This is well established in the literature (De Wit, 1965; Norman and Arkebauer, 1991; Sinclair *et al.*, 1992; Hammer and Wright, 1994; Bange *et al.*, 1997; Rosati *et al.*, 2004) and is due to the curvature of the response of leaf photosynthesis to PAR.

In conclusion, the smaller reduction of canopy PRUE (i.e. 6·3 %) compared with the 20 % reduction in leaf absorptance was due to two main factors. The first was that reducing PAR decreases photosynthesis less that proportionally (in our example the reduction was 11·3 %). The second factor is that kaolin application favourably alters the light distribution within the canopy, so that the final loss in PRUE is even less (in our example it was 6·3 %).

Effect of kaolin application on canopy photosynthesis

Combining eqn (4), the 6·3 % reduction in PRUE (i.e. $E_{HL,R80} = 0{\cdot}937E_{HL,R100}$, Fig. 5), the 20 % reduction in leaf absorptance (i.e. $S_{leaf,K} = 0{\cdot}8\ S_{leaf,C}$) and the 7 % reduction in canopy-absorbed PAR for both almond and walnut (eqns 9 and 10), we obtained:

$$A_{n,K} = \frac{(0{\cdot}93R_{abs,C})(0{\cdot}937E_{HL,R100})}{(0{\cdot}8S_{leaf,C})} \qquad (11)$$

which gives $A_{n,K} = 1{\cdot}09A_{n,C}$ for both species.

This increase must not be taken quantitatively since we estimated a 20 % loss in PAR absorption by the leaves, but did not measure it. In the literature this loss has been found to range from 20–40 % (Abou-Khaled *et al.*, 1970; Moreshet *et al.*, 1979; Wünsche *et al.*, 2004; Rosati *et al.*, 2006). We therefore ran the model also assuming a 30 and 40 % loss. For instance, assuming a 40 % loss, the second term of eqn (11) becomes $0{\cdot}844E_{HL,R100}$ while the final term becomes, by definition, $0{\cdot}6S_{leaf,C}$, giving $A_{n,K} = 1{\cdot}37A_{n,C}$ (i.e. a 37 % increase in canopy photosynthesis). Thus, whatever the correct loss in leaf absorption was, it can be concluded that modelled canopy photosynthesis increases with kaolin despite the reduction in both canopy PAR absorption and PRUE.

This apparent contradiction can be explained by considering that the PRUE is expressed on an incident PAR basis. While assuming a 20 % loss in PAR absorption by the leaves, the PRUE decreased by 6·3 % with kaolin application (i.e. $E_{HL,R80} = 0{\cdot}937E_{HL,R100}$; Fig. 5); the PAR incident on the leaves increased more than proportionally, especially on those in the inner-canopy (Fig. 2A, B), due to the increased reflection of PAR from kaolin-coated leaves.

The increase in incident PAR can be calculated independently of the data from the photosensors in Fig. 2, as the ratio between the first and last term in eqn (11): the total PAR incident within the canopy increased with kaolin application by 16·2 % (0·93/0·8), more than compensating for the 6·3 % decrease in PRUE per unit of incident PAR. As mentioned, this calculation was independent of the PAR data measured with the photosensors, having been obtained from measurements of canopy PAR interception and transmission and by assuming that kaolin application increased leaf PAR reflection (and decreased PAR absorption) by 20 %. Similar results were obtained with a 30 or 40 % reduction in PAR absorption.

Another way to explain the increase in estimated canopy photosynthesis with kaolin application, despite the decreases in both PRUE (per unit of incident PAR) and canopy PAR absorption, is to consider the PRUE per unit of PAR absorbed, which can be obtained as the ratio between the last two factors in eqn (11): the PRUE per unit of absorbed PAR increased with kaolin application by 17·1 % (0·937/0·8) for both species, more than compensating for the 7 % decrease in canopy PAR absorption.

Our results were obtained from well-irrigated trees and no water stress was considered. In the case of water stress, if kaolin applications have the ability to reduce the effect of the stress on crop performance, as often speculated (Jifon and Syvertsen, 2003; Glenn *et al.*, 2001, 2003), these positive effects would add to those here reported, which were based solely on PAR distribution and its effects on canopy PRUE and photosynthesis.

CONCLUSIONS

We tested the hypothesis that the maintenance or increase in canopy photosynthesis with kaolin application, despite the decrease in leaf photosynthetic activity at any given PAR, could result from better light distribution of PAR within the canopy. The data prove that kaolin application does alter light distribution within the canopy, increasing incident radiation especially on inner-canopy leaves. This increase partly compensates for the reduction of PAR absorption of individual leaves treated with kaolin so that, for the whole canopy, PAR absorption is reduced only minimally. It is further demonstrated that the altered PAR distribution improves the PRUE per unit of PAR absorbed, more than compensating for the minor loss in light absorption by the whole canopy.

The data demonstrate, therefore, that canopy photosynthesis may be improved with kaolin application, despite the apparent decrease in photosynthesis of individual leaves when measured at the same PAR as control leaves. This explains the contradiction in the literature of increased yield with kaolin application (Stanhill *et al.*, 1976; Moreshet *et al.*, 1979; Soundara Rajan *et al.*, 1981; Srinivasa Rao, 1985; Glenn *et al.*, 2001), despite an apparent reduction in leaf photosynthesis (Moreshet *et al.*, 1979; Glenn *et al.*, 2003; Grange *et al.*, 2004; Wünsche *et al.*, 2004; Rosati *et al.*, 2006).

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APPENDIX

List of abbreviations

$A_{\mathrm{n,C}}$	Daily net photosynthesis of canopy for control trees (mmol $\mathrm{m^{-2}\ d^{-1}}$)
$A_{\mathrm{n,K}}$	Daily net photosynthesis of canopy for kaolin-treated trees (mmol $\mathrm{m^{-2}\ d^{-1}}$)
E	Photosynthetic radiation use efficiency over one day: net photosynthesis per unit of incident photosynthetically active radiation (mmol $\mathrm{mol^{-1}}$)
E_{50L}	Photosynthetic radiation use efficiency calculated with the 50-leaf model the day before kaolin application (mmol $\mathrm{mol^{-1}}$)
E_{HL}	Photosynthetic radiation use efficiency calculated with the hypothetical-leaf model the day before kaolin application (mmol $\mathrm{mol^{-1}}$)
$E_{\mathrm{50L,R100}}$	Photosynthetic radiation use efficiency calculated with the 50-leaf model the day after kaolin application, using the photosynthetically active radiation incident on leaves as measured by the photosensors (mmol $\mathrm{mol^{-1}}$)
$E_{\mathrm{50L,R80}}$	Photosynthetic radiation use efficiency calculated with the 50-leaf model the day after kaolin application, assuming a 20 % reduction in photosynthetically active radiation incident on leaves (mmol $\mathrm{mol^{-1}}$)
$E_{\mathrm{HL,R100}}$	Photosynthetic radiation use efficiency calculated with the hypothetical-leaf model the day after kaolin application, using the incident photosynthetically active radiation as obtained from the weather station (mmol $\mathrm{mol^{-1}}$)
$E_{\mathrm{HL,R80}}$	Photosynthetic radiation use efficiency calculated with the hypothetical-leaf model after kaolin application, assuming a 20 % reduction in the incident photosynthetically active radiation as obtained from the weather station (mmol $\mathrm{mol^{-1}}$)
R	Photosynthetically active radiation (μmol $\mathrm{m^{-2}\ s^{-1}}$)
R_{inc}	Daily incident photosynthetically active radiation (mol $\mathrm{m^{-2}\ d^{-1}}$)
$R_{\mathrm{tr,C}}$	Fraction of incident photosynthetically active radiation transmitted by the canopy of control trees (no units)
$R_{\mathrm{tr,K}}$	Fraction of incident photosynthetically active radiation transmitted by the canopy of kaolin-treated trees (no units)

$R_{\mathrm{ref,C}}$	Fraction of incident photosynthetically active radiation reflected by the canopy of control trees (no units)
$R_{\mathrm{ref,K}}$	Fraction of incident photosynthetically active radiation reflected by the canopy of kaolin-treated trees (no units)
$R_{\mathrm{abs,C}}$	Daily photosynthetically active radiation absorbed by the canopy of control trees (mol $\mathrm{m^{-2}\ d^{-1}}$)
$R_{\mathrm{abs,K}}$	Daily photosynthetically active radiation absorbed by the canopy of kaolin treated trees (mol $\mathrm{m^{-2}\ d^{-1}}$)
$S_{\mathrm{leaf,C}}$	Leaf absorption as fraction of incident photosynthetically active radiation for control leaves (no units)
$S_{\mathrm{leaf,K}}$	Leaf absorption as fraction of incident photosynthetically active radiation for kaolin-treated leaves (no units)