

Physiological Effects of Kaolin Applications in Well-irrigated and Water-stressed Walnut and Almond Trees

A. ROSATI^{1,*}, S. G. METCALF², R. P. BUCHNER³, A. E. FULTON³ and B. D. LAMPINEN²

¹*Istituto Sperimentale per l'Olivicoltura, Via Nursina 2, 06049 Spoleto, (PG) Italy*, ²*Department of Plant Sciences, University of California, Mail stop #2, One Shields Avenue, Davis, CA 95616, USA* and

³*University of California Cooperative Extension, Tehama County, 1754 Walnut Street, Red Bluff, CA 96080, USA*

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• **Background and Aims** Kaolin applications have been used to mitigate the negative effects of water and heat stress on plant physiology and productivity with variable results, ranging from increased to decreased yields and photosynthetic rates. The mechanisms of action of kaolin applications are not clear: although the increased albedo reduces leaf temperature and the consequent heat stress, it also reduces the light available for photosynthesis, possibly offsetting benefits of lower temperature. The objective of this study was to investigate which of these effects are prevalent and under which conditions.

• **Methods** A 6% kaolin suspension was applied on well-irrigated and water-stressed walnut (*Juglans regia*) and almond (*Prunus dulcis*) trees. Water status (i.e. stem water potential, Ψ_s), gas exchange (i.e. light-saturated CO_2 assimilation rate, A_{\max} ; stomatal conductance, g_s), leaf temperature (T_l) and physiological relationships in treated and control trees were then measured and compared.

• **Key Results** In both species, kaolin did not affect the daily course of Ψ_s whereas it reduced A_{\max} by 1–4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ throughout the day in all combinations of species and irrigation treatments. Kaolin did not reduce g_s in any situation. Consequently, intercellular CO_2 concentration (C_i) was always greater in treated trees than in controls, suggesting that the reduction of A_{\max} with kaolin was not due to stomatal limitations. Kaolin reduced leaf temperature (T_l) by about 1–3 °C and leaf-to-air vapour pressure difference (VPD_l) by about 0.1–0.7 kPa. A_{\max} was lower at all values of g_s , T_l and VPD_l in kaolin-treated trees. Kaolin affected the photosynthetic response to the photosynthetically active radiation (PAR) in almond leaves: kaolin-coated leaves had similar dark respiration rates and light-saturated photosynthesis, but a higher light compensation point and lower apparent quantum yield, while the photosynthetic light-response curve saturated at higher PAR. When these parameters were used to model the photosynthetic response curve to PAR, it was estimated that the kaolin film allowed 63% of the incident PAR to reach the leaf.

• **Conclusions** The main effect of kaolin application was the reduction, albeit minor, of photosynthesis, which appeared to be related to the shading of the leaves. The reduction in T_l and VPD_l with kaolin did not suffice to mitigate the adverse effects of heat and water stress on A_{\max} .

Key words: *Juglans regia*, kaolin particle film, photosynthesis, *Prunus dulcis*, stomatal conductance, water potential, stress.

INTRODUCTION

Particle film applications, including kaolin, have been used to mitigate the negative effects of water and heat stress on plant physiology and productivity. Results have often been contradictory, as such applications resulted at times in increased yield, as in sorghum (Stanhill *et al.*, 1976), cotton (Moreshet *et al.*, 1979), tomato (Srinivasa Rao, 1985) and peanut (Soundara Rajan *et al.*, 1981), and at other times in no effect or a reduction of yield, as in cotton (Showler, 2002) and pepper (Russo and Díaz-Pérez, 2005).

Most of the early work in this area was done in annual crops. More recently, the application of a particular kaolin product (Surround WP, Engelhard, Iselin, NJ, USA) has been found to be beneficial in pest control on fruit tree species (Glenn *et al.*, 1999; Thomas *et al.*, 2004). This material has also been found to improve yield, fruit colour and size, as well as the instantaneous rate of net photosynthesis of leaves at saturating light (A_{\max}) in apple (Glenn *et al.*, 2001). A revival of studies on kaolin

application has since occurred with, again, contradictory results. Kaolin applications were found to improve A_{\max} in apple but only under high temperature and vapour pressure difference (Glenn *et al.*, 2003), and other authors found no effect or even a reduction in either yield or A_{\max} or both (Schupp *et al.*, 2002; Grange *et al.*, 2004; Wünsche *et al.*, 2004). Little data are available on other tree species: kaolin improved A_{\max} and stomatal conductance (g_s) in citrus at midday but not in the morning (Jifon and Syvertsen, 2003) whereas no effect was found on pecan (Lombardini *et al.*, 2004).

Some hypotheses have been formulated to explain the different results. Particle films have been shown to reduce the light available to the leaf by increasing light reflection (Abou-Khaled *et al.*, 1970; Wünsche *et al.*, 2004). This can reduce leaf A_{\max} under optimal conditions for photosynthesis. However, at high temperature, A_{\max} may be more limited by the heat stress than by low light so that the reduction in leaf temperature, induced by the kaolin film, could more than compensate for the negative effect of reduced light (Glenn *et al.*, 2003). This hypothesis has been confirmed by Grange *et al.* (2004), who showed that

* For correspondence. E-mail adolfo.rosati@entecra.it

kaolin applications on apple trees reduced A_{\max} in all cases except in outer-canopy leaves exposed to high irradiance under high temperature and high leaf-to-air vapour pressure difference (VPD_1).

Similar reductions in A_{\max} with kaolin application in apple were found by Wünsche *et al.* (2004), who attributed them to a 20% decrease in absorbed photosynthetically active radiation (PAR) to the leaf. The loss of PAR absorption was entirely due to increased PAR reflection. The authors proposed that the measured loss in A_{\max} was due to the non-saturating light used ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) when measuring A_{\max} on kaolin-coated leaves, which, being shaded by the particle film, needed greater light intensities to reach saturation.

The objectives of the present study were to test (a) whether kaolin applications reduce leaf photosynthesis through physical shading of the leaf and, if so, to quantify the effect; (b) whether, and under which conditions, the mitigation of the heat stress compensates for the shading effect. To test possible interactions between kaolin application and water stress, in different species, kaolin was applied on well-irrigated and water-stressed almond and walnut trees.

MATERIALS AND METHODS

Plant material

The experiment was carried out during summer 2003 on an 8-year-old almond [*Prunus dulcis* (Mill) D.A. Webb 'Nonpareil'] orchard in Solano county, California, and a 10-year-old walnut (*Juglans regia* L. 'Chandler') orchard in Tehama county, California. Tree spacing was 6×7 m for almond and 4.7×7.3 m for walnuts. Almonds were trained to an open vase while walnuts were trained to a hedgerow configuration and hedged on alternate sides each year. The crops received routine horticultural care suitable for commercial production, including fertilization, irrigation, and weed and pest control.

Both the walnut and the almond orchards were split into well-irrigated (W) and water-stressed (S) treatments. The walnut orchard was irrigated every 2–3 d with micro-sprinklers providing about 100% crop evapo-transpiration (ETc) in the W treatment and 50% ETc in the S treatment. The almond orchard was irrigated every 2 weeks with about 100% ETc until 1 month prior to the experiment, then irrigation continued only on the W treatment.

On 17 July in almond, and on 18 August in walnut, a 6% kaolin water suspension (Surround WP), with no adhesive or other compounds, was sprayed on foliage to runoff from above the canopies, on an area of the orchard (three rows by four trees for a total of 12 trees) on both the W and the S treatments. The day after spraying, water status and gas exchange were measured on the two central trees of each kaolin-sprayed (K) area and on two control (C) trees in both the well-irrigated and the water-stressed part of the orchard. In total, eight trees were sampled for each species, two from each combination of treatments: well-irrigated plus kaolin (WK), well-irrigated control

(WC), water-stressed plus kaolin (SK) and water-stressed control (SC).

Water status measurements

For both almond and walnut, stem water potential (Ψ_s) was measured throughout the day with the bagged leaf technique (McCutchan and Shackel, 1992) and a Scholander-type pressure chamber, using two leaves per tree (i.e. four readings per combination of treatments) at each measuring time. Leaves chosen were situated in shaded positions near the main trunk.

Gas exchange measurements

A_{\max} , g_s and intercellular CO_2 concentration (C_i) were measured with a portable computerized open-system IRGA (LI-6400, LI-COR. Inc., Lincoln, NB, USA). Leaf temperature (T_l) and VPD_1 in the leaf chamber were also recorded. A red–blue light source (6400-02 light-emitting diode) under software control was mounted on the leaf chamber as the source of light, which was set at a PAR of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Leaves were kept in the chamber for 1–3 min until photosynthesis was constant.

Measurements were taken on four leaves per tree on each of the two trees per treatment, at each measuring time, five times per day. Upper-canopy leaves that were exposed to full sunlight prior to measurements were chosen. The chamber was kept in the shade when not in use, to keep it at ambient temperature and to avoid overheating.

Leaf photosynthetic response to light

On 19 July, 1 d after the gas exchange measurements described above, the photosynthetic response to light of four leaves from each combination of treatments was measured in almond. Measurements were taken between 0900 and 1300 h on the same type of leaves (i.e. upper-canopy leaves in full sun). The kaolin-sprayed leaves were chosen among those with more uniform coating. The light-response curve was obtained with PAR values of 2500, 2000, 1500, 1000, 500, 250, 125, 50, 25 and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Leaves were allowed to stabilize at each light step for a minimum of 1 min and then data were logged after steady-state conditions were achieved. From each curve, the following parameters of the leaf photosynthetic response to PAR were obtained and averaged for the eight kaolin-sprayed leaves and the eight control leaves (data within each irrigation treatment were pooled because there was no statistical effect of irrigation): dark respiration rate (R_d), compensation point (CP), apparent quantum yield (Φ), net photosynthetic rate at $2000 \mu\text{mol mol}^{-1} \text{s}^{-1}$ of PAR ($A_{\max 2000}$), at $2500 \mu\text{mol mol}^{-1} \text{s}^{-1}$ of PAR ($A_{\max 2500}$) and their ratio ($A_{\max 2000}/A_{\max 2500}$). Differences between kaolin and control treatments for each parameter were assessed via analysis of variance. The average values of each parameter was then used in the Thornley (1976) model of the leaf photosynthetic

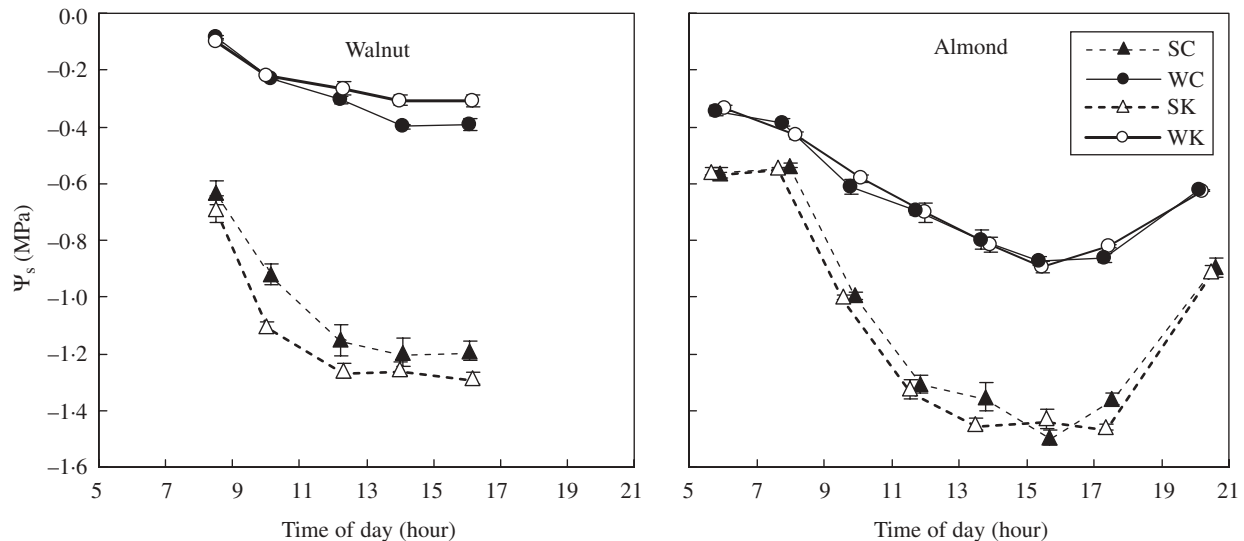


FIG. 1. Daily course of stem water potential (Ψ_s) in water-stressed (S) and well-irrigated (W) walnut and almond trees, sprayed with kaolin (K) or controls (C). Each point is the average four measurements. Bars indicate standard errors. When not visible, bars are smaller than the symbols.

response to PAR to describe the two curves for the kaolin-coated and control leaves. Assuming that leaf physiology did not change overnight, and that the apparent difference in photosynthetic response to PAR was solely due to the physical presence of the film, the modelled curves were then used to estimate the reduction in incident PAR due to the kaolin film. This was done by assuming that only a constant fraction of the light incident over a kaolin-coated leaf would actually reach the leaf. The fractional value that would make the two curves overlap provided an estimate of the shading effect of the kaolin film.

RESULTS

Stem water potential

Within each species, the daily course of Ψ_s was greatly affected by the water stress (Fig. 1). Kaolin application had no effect on Ψ_s in almond. In walnut, kaolin appeared occasionally to increase Ψ_s (in the W treatment), or decrease it (in the S treatment), but such patterns were observed on the same trees also the day before kaolin was applied (data not shown).

Gas exchange

In walnut, A_{\max} was highest in the early morning and decreased throughout the day, for both the S and the W treatments (Fig. 2A). A_{\max} was always lower for the S treatments, especially in the afternoon. Kaolin application reduced A_{\max} (by up to $4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) within each irrigation treatment, especially in the morning when A_{\max} was high, whereas in the afternoon this effect tended to disappear in the W treatment and disappeared completely in the S treatment. The average reduction in A_{\max} during the day was minor compared with the reduction due to water stress and was $1.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the S treatments and $2.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the W treatment.

In almond, A_{\max} and gas exchange in general were not affected by the water stress imposed, and therefore data were pooled for the irrigation treatments within each kaolin treatment (i.e. kaolin-sprayed, K, and control, C; Fig. 2B). Kaolin application reduced almond A_{\max} at all times, with an average loss for the whole day of $1.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Stomatal conductance (g_s) showed daily trends similar to A_{\max} in both species, with the exception of lower values in the morning measurement in the W treatments on walnut (Fig. 2C, D). Kaolin application had no effect on g_s for either species or treatment, except around midday in the well-irrigated walnut trees where g_s was 25% higher, but this was true also on the day before kaolin was applied (data not shown).

Intercellular CO_2 concentration (C_i) was greatly reduced with water stress in walnut while the irrigated walnut and the almond trees had similar C_i values (Fig. 2E, F). Kaolin application increased C_i in all cases except for two out of five measurements in the S treatment in walnut. The average daily increase in C_i with kaolin was $28 \mu\text{mol mol}^{-1}$ in the S and $19 \mu\text{mol mol}^{-1}$ in the W treatments for walnut and $10 \mu\text{mol mol}^{-1}$ for almond.

Leaf temperature and VPD_l

Leaf temperature (T_l) and leaf-to-air vapour pressure deficit (VPD_l) increased in all cases from early morning to midday or early afternoon, then decreased (Fig. 3). Both T_l and VPD_l were greatly increased by water stress in walnut. Kaolin application slightly reduced both T_l (by $2\text{--}3^\circ\text{C}$) and VPD_l (by $0.1\text{--}0.7 \text{ kPa}$) in all cases.

Physiological relationships

A_{\max} and g_s were strongly and curvilinearly related in all cases (Fig. 4). In walnut, water stress increased the

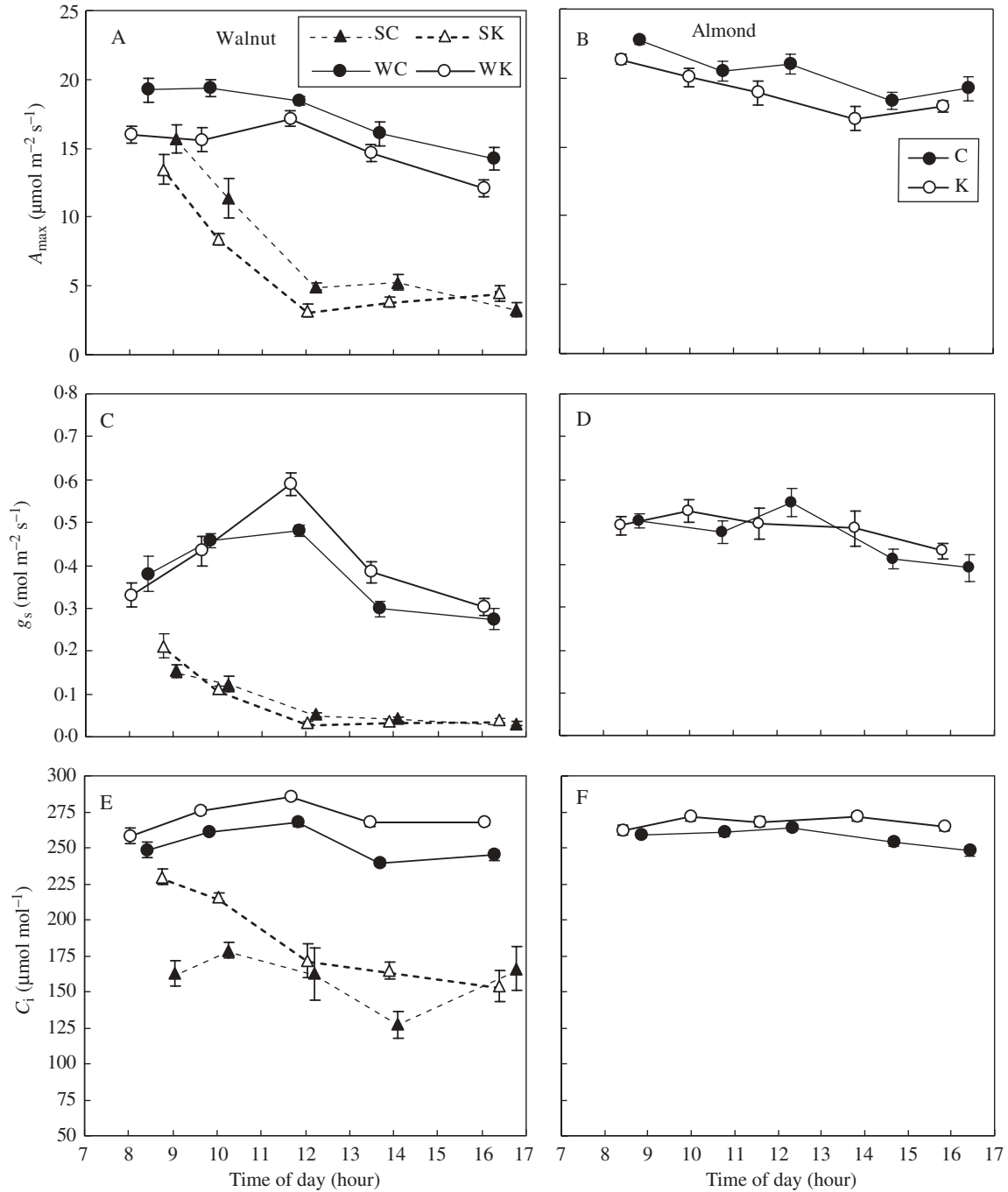


FIG. 2. Daily course of light-saturated net CO_2 assimilation rate (A_{max}), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) in water-stressed (S) and well-irrigated (W) walnut and almond trees, sprayed with kaolin (K) or controls (C). Each point is the average of eight measurements in walnut and 16 measurements in almond where W and S treatments were pooled. Bars indicate standard errors. When not visible, bars are smaller than the symbols.

slope of the relationships in both the K and the C treatments. Kaolin application reduced A_{max} at any g_s in all combinations of treatments.

In walnut, the W treatments had higher A_{max} and g_s at any temperature (Fig. 5A, C) and any VPD_1 (Fig. 6A, C) than the S treatments. Kaolin application reduced the A_{max} response curve to temperature (Fig. 5A, B), and VPD_1 (Fig. 6A, B) in all treatments. Kaolin application had no effect on the g_s vs. T_1

relationship (Fig. 5C, D), nor on the g_s vs. VPD_1 relationship (Fig. 6C, D).

Leaf photosynthetic response to light

Kaolin application did not affect R_d , nor $A_{max2500}$, but significantly reduced $A_{max2000}/A_{max2500}$ and Φ , while CP was significantly increased (Table 1).

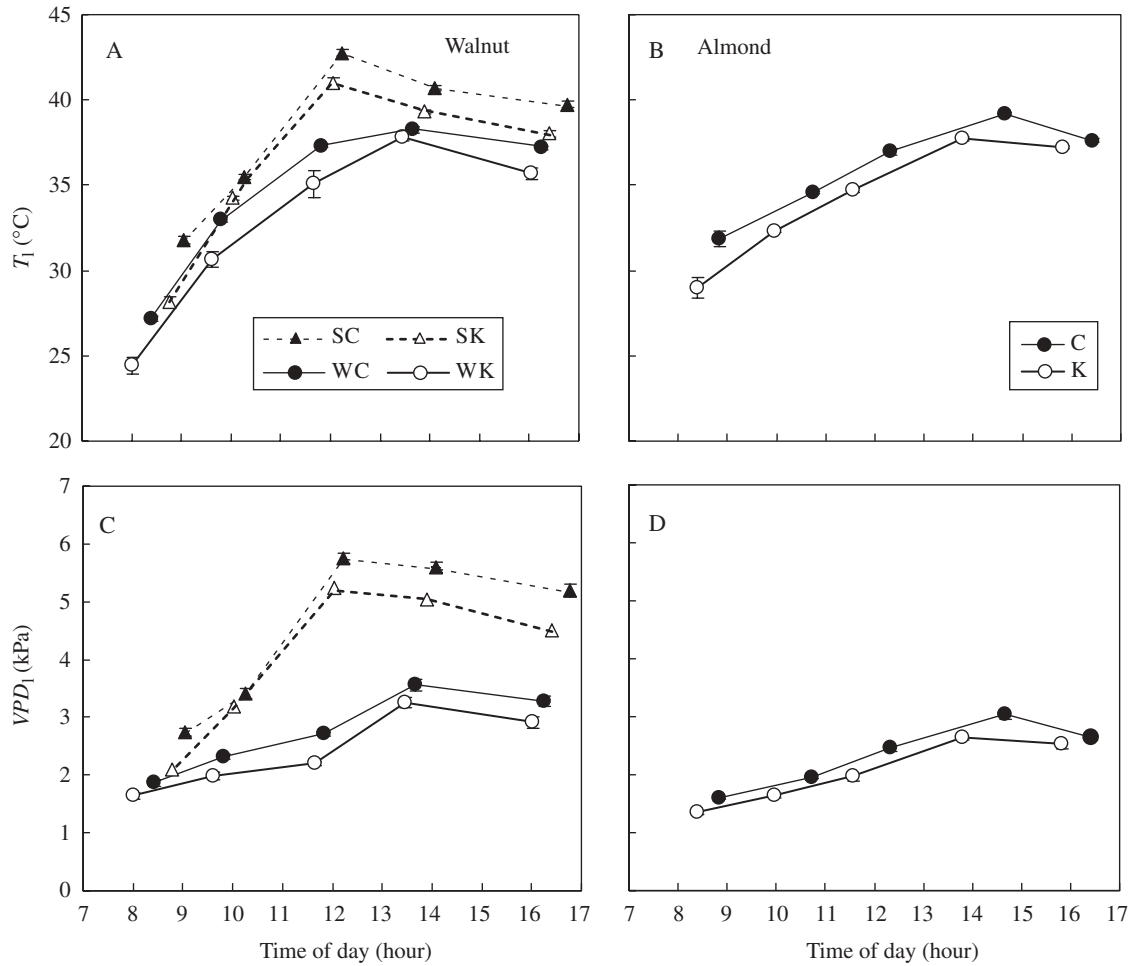


FIG. 3. Daily course of leaf temperature (T_l) and leaf-to-air vapour pressure difference (VPD_l). Symbols and lines as in Fig. 2.

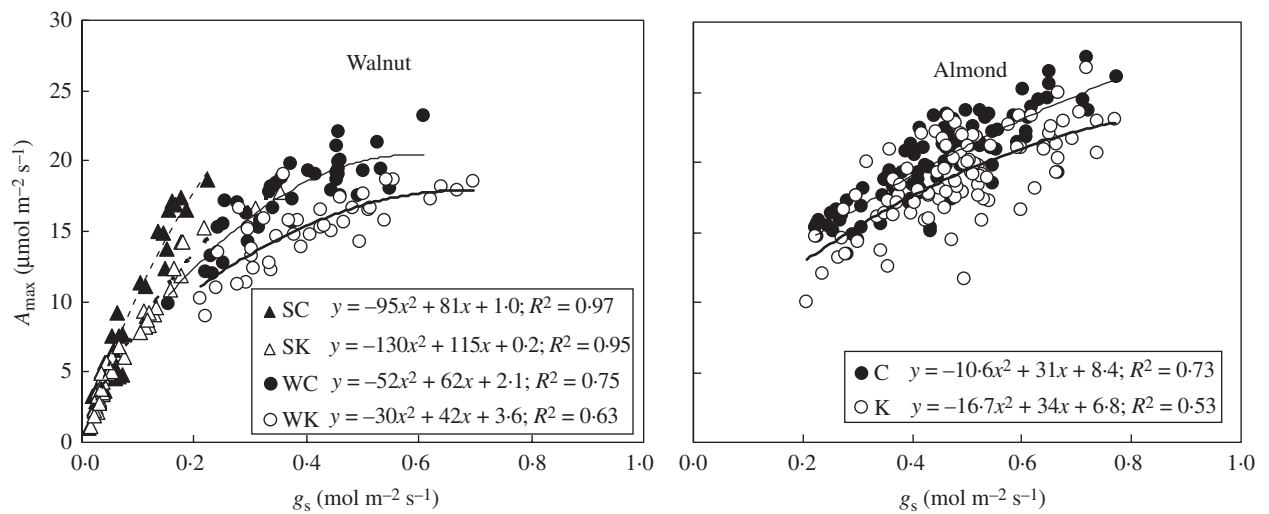


FIG. 4. Relationship between light-saturated photosynthesis (A_{max}) and stomatal conductance (g_s) in water-stressed (S) and well-irrigated (W) walnut and almond trees sprayed with kaolin (K) or controls (C). In walnut, the lines are polynomial fits to the SC (dotted, thin line), the SK (dotted, thick line), the WC (solid thin line) and the WK (solid thick line) data. In almond the solid thin line is a polynomial fit to the C data (i.e. WC and SC pooled), and the solid thick line is a polynomial fit to the K data (i.e. WK and SK pooled). The equations of the fits are shown in the graphs near the respective symbols. Each point represents one measurement.

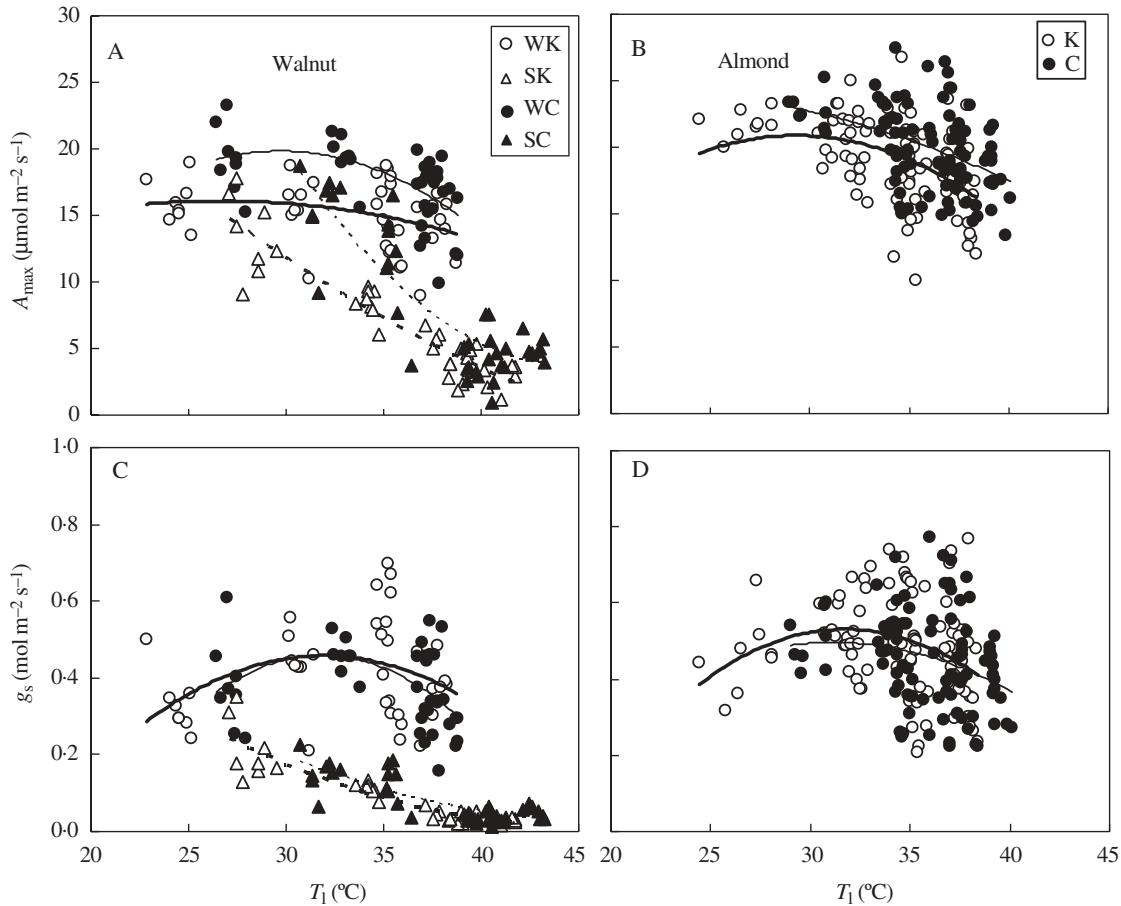


FIG. 5. Relationship between light-saturated photosynthesis (A_{\max}) and stomatal conductance (g_s), and leaf temperature (T_l). Symbols and lines as in Fig. 4. The equations for walnut are: WC, $A_{\max} = -0.058(T_l)^2 + 3.5(T_l) - 31.6$, $R^2 = 0.32$, and $g_s = -0.0033(T_l)^2 + 0.208(T_l) - 2.86$, $R^2 = 0.18$; WK, $A_{\max} = -0.017(T_l)^2 + 0.90(T_l) + 4.2$, $R^2 = 0.10$ and $g_s = -0.0021(T_l)^2 + 0.13(T_l) - 1.67$, $R^2 = 0.12$; SC, $A_{\max} = 0.074(T_l)^2 - 6.6(T_l) + 151$, $R^2 = 0.76$ and $g_s = 0.0007(T_l)^2 - 0.061(T_l) + 1.4$, $R^2 = 0.66$; SK, $A_{\max} = 0.015(T_l)^2 - 1.89(T_l) + 55$, $R^2 = 0.86$ and $g_s = 0.0007(T_l)^2 - 0.062(T_l) + 1.4$, $R^2 = 0.83$. The equations for almond are: C, $A_{\max} = -0.0177(T_l)^2 + 0.72(T_l) + 17.1$, $R^2 = 0.18$ and $g_s = -0.0016(T_l)^2 + 0.101(T_l) - 1.08$, $R^2 = 0.07$; K, $A_{\max} = -0.057(T_l)^2 + 3.31(T_l) - 27.6$, $R^2 = 0.21$ and $g_s = -0.0027(T_l)^2 + 0.172(T_l) - 2.19$, $R^2 = 0.09$.

The modelled leaf photosynthetic response to PAR was different for the kaolin-coated and the control leaves (Fig. 7A). Assuming that only 63% of the PAR incident on the kaolin-coated leaves actually reached the leaf surface, the modelled curves for the two treatments overlapped perfectly at any PAR (Fig. 7B).

DISCUSSION

The reduction of A_{\max} with kaolin was only minor compared with the reduction with water stress: the average A_{\max} reduction was 1.4, 2.4 and 1.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, in well-irrigated walnut, and water-stressed walnut and almond (W and S treatments pooled). Wünsche *et al.* (2004) found that A_{\max} was significantly reduced by 2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at low average ambient temperature (their table 2), but not significantly reduced at high temperature (i.e. 34–31 °C). Indeed, A_{\max} was reduced at high temperature by 1.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (which is in

the range of our measurements), but the reduction was not statistically significant.

Photosynthesis was lower with kaolin at any g_s (Fig. 4), suggesting that the loss in A_{\max} was not related to stomatal blockage as found in tomato (Srinivasa Rao, 1986), or stomatal closure, as confirmed by the higher C_i (Fig. 2E, F). In fact, kaolin did not affect g_s , as supported also by the fact that tree water status (i.e. Ψ_s) was not affected, implying that whole tree transpiration was probably unaffected as well.

Reductions in A_{\max} were also not due to an effect of kaolin application on the environmental parameters that could affect photosynthesis (i.e. T_l and VPD_l) as A_{\max} was lower at all T_l (Fig. 5) and VPD_l (Fig. 6). Outside the leaf chamber, most leaves are exposed to less than saturating PAR and therefore to lower temperature and VPD, and our data cannot easily be scaled up to the whole canopy. However, at least for the conditions of the leaf chamber, kaolin did reduce temperature, but this did not compensate for the loss in A_{\max} . This would be even more true for leaves outside the chamber, exposed to lower PAR and

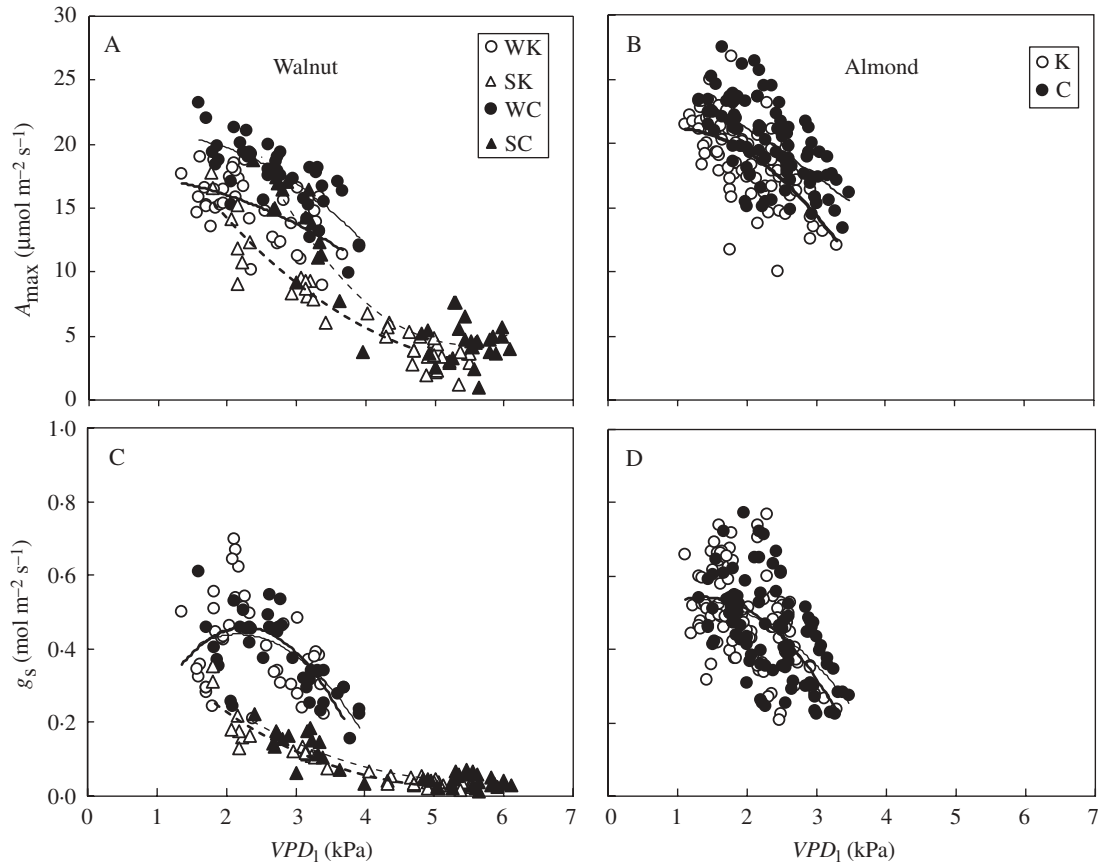


FIG. 6. Relationship between light-saturated photosynthesis (A_{\max}) and stomatal conductance (g_s), and leaf-to-air vapour pressure difference (VPD_1). Symbols and lines as in Fig. 4. The equations for walnut are: WC, $A_{\max} = -0.93(T_1)^2 + 1.9(T_1) + 19.7$, $R^2 = 0.58$, and $g_s = -0.0818(T_1)^2 + 0.354(T_1) + 0.05$, $R^2 = 0.47$; WK, $A_{\max} = -0.50(T_1)^2 + 0.27(T_1) + 17.5$, $R^2 = 0.33$ and $g_s = -0.123(T_1)^2 + 0.56(T_1) - 0.17$, $R^2 = 0.20$; SC, $A_{\max} = 1.61(T_1)^2 - 17.6(T_1) + 52$, $R^2 = 0.88$ and $g_s = 0.015(T_1)^2 - 0.169(T_1) + 0.52$, $R^2 = 0.81$; SK, $A_{\max} = 0.73(T_1)^2 - 8.59(T_1) + 28.5$, $R^2 = 0.91$ and $g_s = 0.0215(T_1)^2 - 0.216(T_1) + 0.58$, $R^2 = 0.89$. The fit equations for almond are: C, $A_{\max} = -0.250(T_1)^2 - 2.51(T_1) + 27.2$, $R^2 = 0.40$ and $g_s = -0.051(T_1)^2 + 0.112(T_1) + 0.48$, $R^2 = 0.30$; K, $A_{\max} = -1.53(T_1)^2 + 2.73(T_1) + 20.0$, $R^2 = 0.38$ and $g_s = -0.085(T_1)^2 + 0.0232(T_1) + 0.38$, $R^2 = 0.28$.

therefore lower temperature and therefore limited even more by light and less by temperature. The loss in A_{\max} , therefore, was probably related to the shading effect of kaolin, as previously suggested (Abou-Khaled *et al.*, 1970; Wünsche *et al.*, 2004).

To test this hypothesis leaf photosynthetic response to PAR was investigated. Kaolin application did not affect R_d nor the light-saturated photosynthetic rate (i.e. net photosynthetic rate at 2500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR, $A_{\max 2500}$), suggesting that kaolin did not interfere with leaf physiology (Table 1). However, kaolin did reduce the $A_{\max 2000}/A_{\max 2500}$ ratio, which implies that an incident PAR of 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was not sufficient to reach saturation in the kaolin-treated leaves, suggesting a strong shading effect of kaolin. This was confirmed by the lower Φ and the higher CP of kaolin-coated leaves. The modelled light-response curves reflected the different response to PAR of the two treatments (Fig. 7A). The kaolin-coated leaf model showed a slower increase in photosynthesis with increasing PAR and reached saturation at higher PAR. At 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR (i.e. the light level used to measure the A_{\max} data in Fig. 2) the difference in photosynthetic rate was about 1 $\mu\text{mol CO}_2$

$\text{m}^{-2} \text{s}^{-1}$, which is close to the average daily difference in almond (i.e. 1.3 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, Fig. 2B).

With the assumption that only 63 % of the incident PAR was able to reach the leaf surface, with the rest being reflected as previously suggested (Abou-Khaled *et al.*, 1970; Wünsche *et al.*, 2004), the two curves overlapped perfectly, suggesting that kaolin reduced incident PAR by 37 %. The perfect overlapping of the curve, at any PAR, suggests that the fraction of PAR transmitted through the kaolin barrier was indeed constant at all PAR fluxes. Thus, the data here confirm previous hypotheses that kaolin applications reduce photosynthetic rates due to the shading effect on the leaves (Abou-Khaled *et al.*, 1970). Using a spectrophotometer, Wünsche *et al.* (2004) found that PAR absorption of leaves was reduced by 20 %, all of the reduction deriving from increased (+20 %) PAR reflection (albedo). In cotton, leaf absorption was reduced by about 35–40 % in the PAR range (Moreshet *et al.*, 1979). The finding herein of a 37 % reduction in PAR incident on the leaf is within the range of previous studies. The variability in the data probably depends on the amount and uniformity of kaolin application on the sampled leaves, which might change with varying leaf

TABLE 1. Parameters of the photosynthetic response curves to photosynthetically active radiation (PAR) for almond leaves

Treatment	R_d ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	CP ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Φ (mol mol^{-1})	$A_{\text{max}2500}$ ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	$A_{\text{max}2000}/A_{\text{max}2500}$ (%)
Kaolin	-1.7	49	0.03	22.3	93
Control	-1.6	29	0.05	22.3	97
Probability	n.s.	$P < 0.01$	$P < 0.01$	n.s.	$P < 0.01$

Parameters are as follows: dark respiration (R_d), compensation point (CP), apparent quantum yield (Φ), net photosynthetic rate at $2500 \mu\text{mol m}^{-2}\text{s}^{-1}$ of PAR ($A_{\text{max}2500}$), and ratio between the photosynthetic rate at 2000 and that at $2500 \mu\text{mol m}^{-2}\text{s}^{-1}$ of PAR ($A_{\text{max}2000}/A_{\text{max}2500}$). Each value is the average of eight measurements.

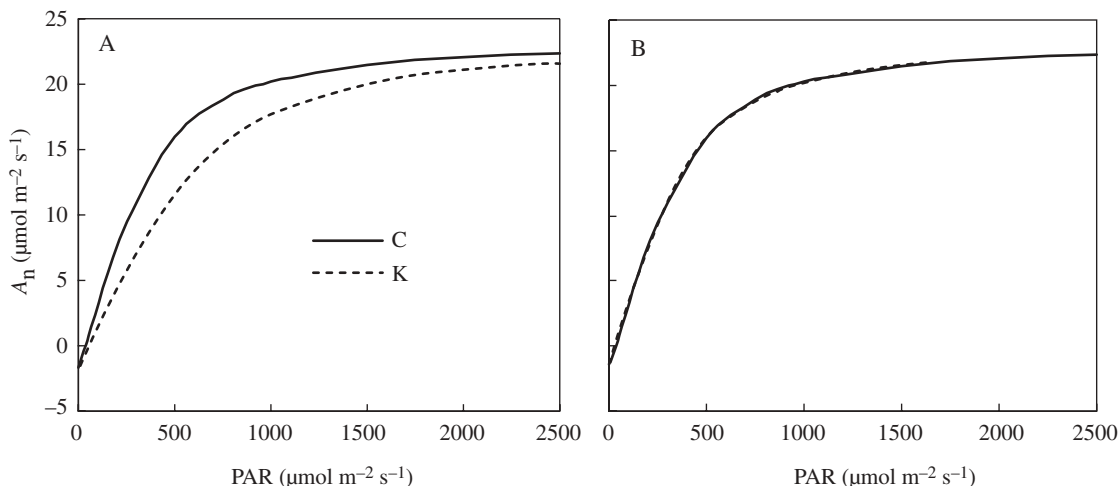


FIG. 7. (A) Response of net photosynthesis (A_n) to photosynthetically active radiation (PAR). The curves represent A_n as modelled using the curve parameters measured on eight kaolin-coated leaves (K) and eight control leaves (C) in almond (see Table 1). (B) Same modelled response curves as in A, but plotting A_n against 63 % of incident PAR for the K treatment. The dotted line is difficult to see because it overlaps with the solid line.

surface characteristics among species and with spraying techniques.

In walnut, the difference in A_{max} between kaolin and control decreased as A_{max} decreased during the day. This was true in both the W and the S treatments, but especially in the latter where A_{max} reached the lowest value at the end of the day and the kaolin treatment (SK) tended to have greater A_{max} than the SC treatment (Fig. 2A). Kaolin applications appear, therefore, to improve photosynthesis at low A_{max} , as was the case in citrus at midday ($A_{\text{max}} < 5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Jifon and Syvertsen, 2003) and apple ($A_{\text{max}} < 8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Glenn *et al.*, 2001), but to reduce it at higher A_{max} , as in citrus in the morning ($A_{\text{max}} \approx 8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Jifon and Syvertsen, 2003) or in other apple orchards ($A_{\text{max}} > 15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Grange *et al.*, 2004; Wünsche *et al.*, 2004). It may be concluded that in species (or under conditions) where A_{max} is low and/or saturates at relatively low PAR, the kaolin-induced reduction in PAR is less important, so that the beneficial mitigation of the heat stress may result in improved A_{max} . At higher A_{max} , the PAR reduction associated with kaolin reduces photosynthesis.

These considerations, however, cannot be scaled up from the leaf to the whole canopy because, in the latter, most leaves are exposed (and adjusted) to less than saturating PAR. The increased albedo with kaolin, at the leaf level, probably improves the light distribution within

the canopy, possibly compensating for the shading effect (Wünsche *et al.*, 2004). Therefore, study of the effect of kaolin applications on whole-canopy gas exchange requires a different approach, which will be undertaken in a further study.

CONCLUSIONS

Kaolin application reduced leaf temperature (T_l) and leaf-to-air vapour pressure difference (VPD_l), but not sufficiently to compensate for the increase in T_l and VPD_l with water stress in walnut. The kaolin-induced reduction in T_l and VPD_l did not mitigate the adverse effects of heat and water stress on A_{max} . Kaolin application did not affect g_s nor Ψ_s . The prevailing effect of kaolin application appeared to be the shading of the leaves and the consequent, albeit minor, reduction of A_{max} , except at very low A_{max} .

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