Improving photosynthetic performance and some fruit quality traits in mango trees by shading

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Abstract

Excess solar radiation under hot climate can lead to decline in photosynthetic activity with detrimental effects on growth and yield. The aim of this study was to evaluate the use of a transparent plastic roof as shading for diurnal changes in photosynthetic gas exchange, chlorophyll fluorescence, fruit set and quality of mango (*Mangifera indica* L.) cv. 'Nam Dok Mai' growth in the field conditions. Fully expanded leaves were examined either shaded by the plastic roof or sunlit under natural conditions. Leaf temperature and leaf-to-air vapour pressure deficit of the shaded leaves measured on the clear day were lowered compared to those of the sunlit leaves. It resulted in increased stomatal conductance and photosynthetic rates of the shaded leaves compared to those of the sunlit leaves, especially from the morning to midday. Furthermore, the reversible decrease of the maximal quantum yield of PSII was more pronounced in the sunlit leaves than that in the shaded ones. Shading increased the total fruit number; the shaded fruits developed better external color than that of the sun-exposed fruits. Our results indicated that shading could maintain the high photosynthetic activity by reducing stomatal limitations for carbon supply and was effective in alleviating the photoinhibitory damage to PSII during bright and clear days with excessive radiation. Finally, shading could increase the number of fruits and improve mango peel color.

Additional key words: chlorophyll fluorescence; excessive irradiation; net photosynthetic rate; photoinhibition.

Introduction

Light energy absorbed by chlorophyll (Chl) molecules in a leaf is used to drive photosynthesis. However, excess radiation can limit photosynthesis which can have a profound impact on agricultural production. Long periods of exposure to high irradiation can lead to temperature stress which may have an impact on gas exchange by altering the leaf-to-air vapour pressure deficit ($VPD_{leaf-air}$). The $VPD_{leaf-air}$ directly influences stomatal conductance (g_s) and indirectly influences CO_2 assimilation *via* an associated change in g_s (Barron-Gafford *et al.* 2007). High $VPD_{leaf-air}$ levels during midday full sunlight resulting in a midday depression of photosynthesis have been observed in various plants (Pettigrew *et al.* 1990). In parallel, the inhibition of photosynthesis of most plants, which encounter supra-optimal solar energy exceeding their

photosynthetic capacity under natural climate condition, is known as photoinhibition. Photoinhibition may be a short-term and reversible or long-term and irreversible event. Reversible photoinhibition is indicative of a protective mechanism for dissipating excess light energy, while irreversible photoinhibition indicates damage to the photosynthetic apparatus (Goh *et al.* 2012).

There have been many research reports observing that cultivation of economic fruit crops under adjusted moderate shading conditions, which prevent excessive radiation above the photosynthetic saturation point, could maintain high photosynthetic activity, decrease photo-inhibition, and improve the yield (Medina *et al.* 2002, Jifon and Syvertsen 2003, Ibrahim and Jaafar 2011). In particular, mango fruit produced under shade cloth had less

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anthracnose and fruit rot disease than that under natural conditions (Juntamanee *et al.* 2013). Changes in the microclimate under shade cloth may also affect photosynthesis and finally the yield. However, the photosynthetic process of mango grown under such circum-stances has not been fully elucidated. Therefore, this study investigated the usefulness of shading on the photosynthesis response of mango as measured by leaf gas exchange and Chl fluorescence.

Materials and methods

Experimental site and plant material: The experiment was undertaken in a commercial orchard in Nakhon Pathom province, Thailand (14°8'N, 100°10'E) during the rainy season. Fifteen-year-old 'Nam Dok Mai' mango trees (*Mangifera indica* L.) were used. Trees were spaced 3 m within rows and 5 m between rows with an irrigation canal of 1 m wide between rows. Fertilizer was applied and insects and diseases were controlled according to re-commendations commonly accepted for mango orchards.

The shading structure was built when mango began flowering and then removed at harvesting time. A plastic shade screen was mounted horizontally 0.5 m above the canopy of ten trees. Another ten trees in the same row were selected and grown without a canopy shade. During the early morning and late afternoon sun light reached the whole canopy of all trees, while at midday, the trees under the screen were completely shaded, whereas the trees outside received full sun light.

Microclimate: In order to assess the effect of radiation transmittance on the microclimatic conditions of mango trees under the plastic roof and in natural open conditions, relative humidity (RH) and air temperature (T_{air}) data logger sensors (*Watchdog 1450; Spectrum Technologies, Inc.,* Aurora, IL, USA) were placed above the plastic roof and at canopy level under the plastic roof. The PPFD was measured using quantum light sensors (*Spectrum Technologies, Inc.*, Aurora, IL, USA) connected to both data loggers at locations close to the data loggers. All data were stored every 15 min. The air vapour pressure deficit (VPD_{air}) was calculated from T_{air} and RH values according to Goudriaan and van Laar (1994).

Gas exchange: Three leaves in each treatment were tagged and diurnal changes in leaf gas exchange were measured at hourly intervals between 08:00–17:00 h on a cloudy day (135-day-old leaves) and on a clear day (180-day-old leaves) using a portable photosynthesis system (*LI-6400; LI-COR Inc.*, Lincoln NE, USA). Each leaf was clamped inside the leaf chamber of the portable photosynthesis system with the upper leaf surface inside the chamber fully exposed to natural PPFD. The flow rate was controlled at 400 µmol mol^{-1}. Each sample set included net photo-synthetic rate (P_N), stomatal conductance (g_s), leaf temperature (T_{leaf}), leaf-to-air vapour pressure deficit ($VPD_{leaf-air}$), and PPFD, while intrinsic water-use effi-ciency (WUE_i) was calculated from these measurements.

Chl fluorescence: The parameters of Chl fluorescence were measured on the same leaves used for the gas-exchange measurements. Measurements were carried out every hour with a pulse-amplitude modulated photo-synthesis yield analyzer (*Mini-PAM; Walz*, Effeltrich, Germany). The minimal (F_0) and maximal fluorescence yield of the dark-adapted state (F_m) emissions were assessed in the leaves after 30 min of dark adaptation and the maximum quantum yield of PSII was calculated as $F_v/F_m = (F_m - F_0)/F_m$. The leaves were then continuously illuminated with a white actinic light at an intensity of 300 µmol(photon) m^{-2} s^{-1} in order to measure F_s and F_m' (steady-state and maximal fluorescence yield of the light-adapted state, respectively). The parameter F_0' (minimal fluorescence yield of the light-adapted state) was estimated (Baker and Rosenqvist 2004). Photochemical quenching coefficient (q_p) was calculated as $q_p = (F_m' - F_m')/(F_m' - F_0')$. Nonphotochemical quenching (NPQ) was calculated from $(F_m - F_m')/F_m'$ (Genty *et al.* 1989). The electron transport rate (ETR) was calculated as $\Delta F/F_m' \times$ PPFD $\times 0.5 \times 0.84$ (Krall and Edwards 1992).

Fruit set and fruit quality: Total numbers of fruits per tree were counted immediately after harvest and the average fruit mass was derived mathematically from the total mass and total number of fruits per tree. After harvesting, 20 fruits from each treatment were randomly collected and the average fruit size was measured using venire caliper.

Twenty representative marketable fruits per treatment were analyzed for fruit quality parameters. Hunter colour parameter *L** (brightness) and *b** (yellowness) were mea-sured on the surface of skin after incubation the fruit for 7 d until a fruit ripening stage using a *Minolta* colorimeter (*model CR-400; Konica Minolta,* Osaka, Japan).

Total soluble solid (TSS) and titratable acidity (TA) of mango fruits were obtained by removal of fruit skin and squeezing the pulp and then filtering the juice. The TSS content was determined using a refractometer (*model DBR35, XS instruments,* Poncarale-BS, Italy) and ex-pressed as °Brix at 20°C. TA was determined by titration with 0.1 M NaOH in the presence of phenolphthaline as the indicatior. The result was calculated in terms of milliequivalents of acid per mililiter.

Statistical analysis: The daily time-course of leaf gas exchange, Chl fluorescence, fruit set, and fruit quality

were analyzed using a *t*-test. Data were presented as means ± standard errors ($n = 3$).

Results

Microclimate: The maximum PPFD outside the plastic roof exhibited a constant trend with an average of 1,800 μmol(photon) m^{-2} s^{-1} except for some cloudy periods (Fig. 1*A*). The radiation under the plastic roof decreased proportionally by about 30%. There were some cloudy periods, when the maximum PPFD did not reach photosynthetic light saturation in mango, which was approximately 800 μmol(photon) m^{-2} s^{-1}. Daytime T$_{air}$ values were similar outside and under the plastic roof with a range from 23.9 to 33.8°C (Fig. 1*B*). Daytime RH ranged from 37 to 100% during the experimental period (Fig. 1*C*). VPD$_{air}$ was not different outside and under the plastic roof and reached a maximum value noticeably on the same day that had high temperature and low humidity (Fig. 1*B,C,D*).

Gas exchange: Diurnal changes in gas exchange were measured on two days selected, with the first being cloudy

(135-day-old leaves) and the second being on a clear day (180-day-old leaves). Regardless of treatments, the mango leaves received lower PPFD on the cloudy day than that of the clear day (Fig. 2*A,B*). The maximum PPFD on the cloudy day reached about 1,100 μmol(photon) m^{-2} s^{-1} and the PPFD under the shade cloth was reduced by 22.2% (Fig. 2*A*). On the clear day, the maximum PPFD outside the roof was about 2,200 μmol(photon) m^{-2} s^{-1} and it was reduced to 1,600 μmol(photon) m^{-2} s^{-1} as a result of shading by the plastic roof (Fig. 2*B*). Diurnal changes in T$_{leaf}$ and VPD$_{leaf-air}$ followed a parallel trend in each other. Regardless of treatments, T$_{leaf}$ and VPD$_{leaf-air}$ on the clear day were higher than that on the cloudy day (Fig. 2*C,D,E,F*). The shade cloth significantly caused a decrease in T$_{leaf}$ and VPD$_{leaf-air}$ on both clear and cloudy measurement days (Fig. 2*C,D,E,F*).

The relationships between P_N and g_s were fitted using linear regression (Microsoft Excel).
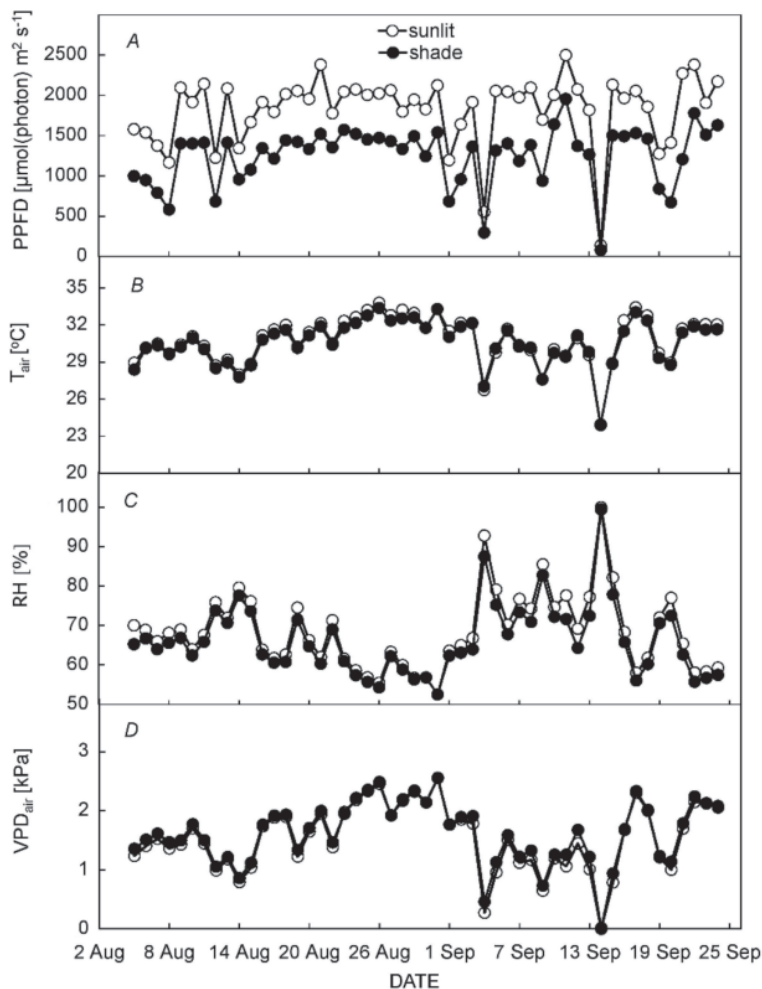

Fig. 1. (*A*) Daily average photosynthetic photon flux density (PPFD), (*B*) average daytime air temperature (T$_{air}$), (*C*) daytime relative humidity (RH), and (*D*) daytime air vapour pressure deficit (VPD$_{air}$) for mango sunlit (O) and shaded under a plastic roof (●).
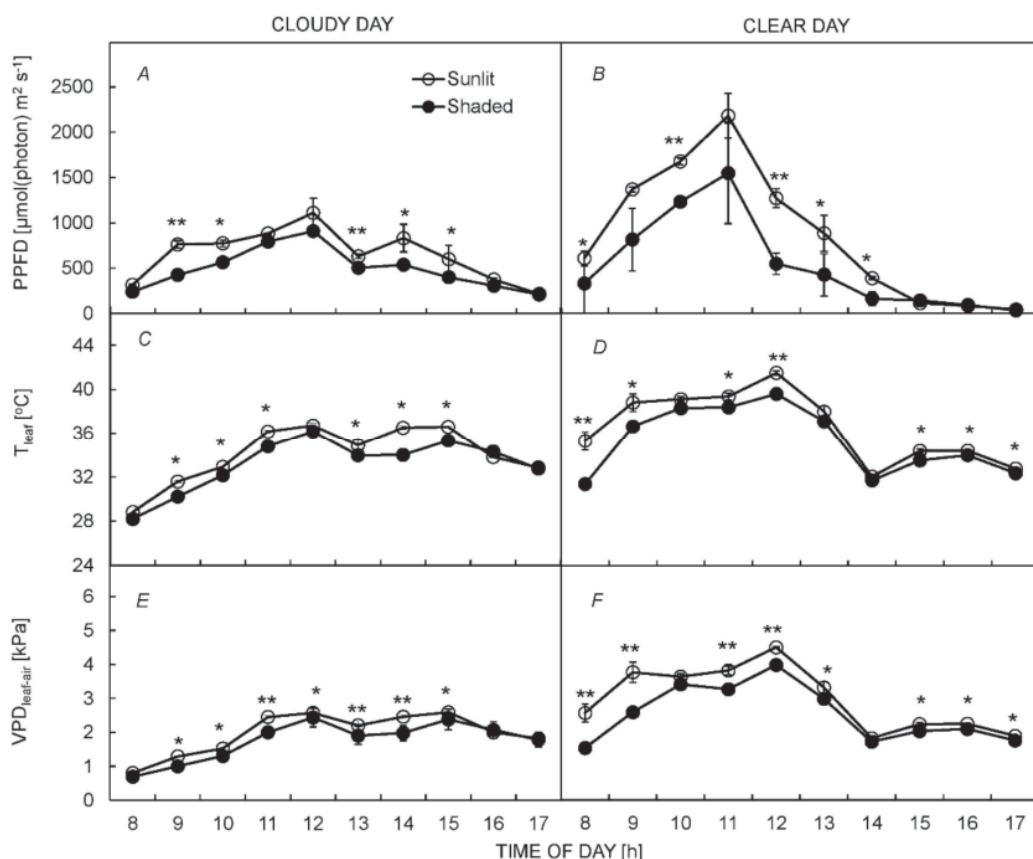
Fig. 2. (*A,B*) Diurnal course of photosynthetic photon flux density (PPFD), (*C,D*) leaf temperature (T_{leaf}), (*E,F*) leaf-to-air vapour pressure deficit ($VPD_{leaf-air}$) of sunlit (○) and shaded leaves (●) of mango measured on the selected cloudy and clear days. *, ** – significant differences between sunlit and shaded at $P \leq 0.05$ and $P \leq 0.01$, respectively. Data are means ± SE, $n = 3$.

Regardless of the treatments, P_N was very low and did not exceed 3.0 μmol m^{-2} s^{-1} (Fig. 3*A,B*). The measurements on the cloudy day revealed the P_N values of the shaded leaves were low and quite stable throughout the day (Fig. 3*A*). A significant increase in the P_N values was observed for the sunlit leaves together with increasing g_s values between 09:00 h and 12:00 h (Fig. 3*A,C*). In the afternoon, the P_N and g_s values of the sunlit leaves decreased and showed the same trend as the shaded leaves. The WUE_i (P_N/g_s) was quite stable throughout the day. However, WUE_i of the sunlit leaves was slightly higher than that for the shaded leaves between 09:00 h and 11:00 h (Fig. 3*E*).

By contrast on the clear day, the P_N and g_s values of the shaded leaves increased sharply in the early morning and remained relatively high between 09:00 h and 11:00 h, while the sunlit leaves had significantly lower P_N and g_s values, especially during the morning until midday (Fig. 3*B,D*). Shade application could maintain WUE_i values higher than under sunlit conditions. Significantly lower P_N/g_s values were also noticed for the sunlit than that for shaded leaves, especially between 09:00 h and 11:00 h (Fig. 3*F*).

There was a difference in the distribution between the P_N and g_s values of the shaded and sunlit leaves measured on the cloudy and clear days. On the cloudy day, there was no alteration in the relationship between the P_N and g_s values, but on the clear day, there were lower P_N and g_s values for the sunlit compared to the shaded leaves (Fig. 4*A,B*).

Chl fluorescence: On the cloudy day, there were no differences in F_v/F_m throughout the measurement period and the F_v/F_m ratio was above 0.77 regardless of the treatments (Fig. 5*A*). On the clear day, when the irradiance was greater, the F_v/F_m ratio of the sunlit leaves dropped drastically after sunrise (Fig. 5*B*). A strong reduction in the value of F_v/F_m of the sunlit leaves to 0.64 was observed at midday. In the shaded leaves, the F_v/F_m values remained near the optimal values of 0.80 except for the slightly lower value of 0.73 at 11:00 h. Regardless of the treatments, the q_p value was lower in the late morning until midday than that in the late afternoon (Fig. 5*C,D*). There was a larger increase of NPQ in both sunlit and shaded leaves on the cloudy day compared to the clear day (Fig. 5*E,F*). The ETR measurements on the cloudy day showed a midday depression for both sunlit and shaded leaves (Fig. 5*G*). On the clear day, the ETR was depressed for both sunlit and shaded leaves during the measurement period (Fig. 5*H*).
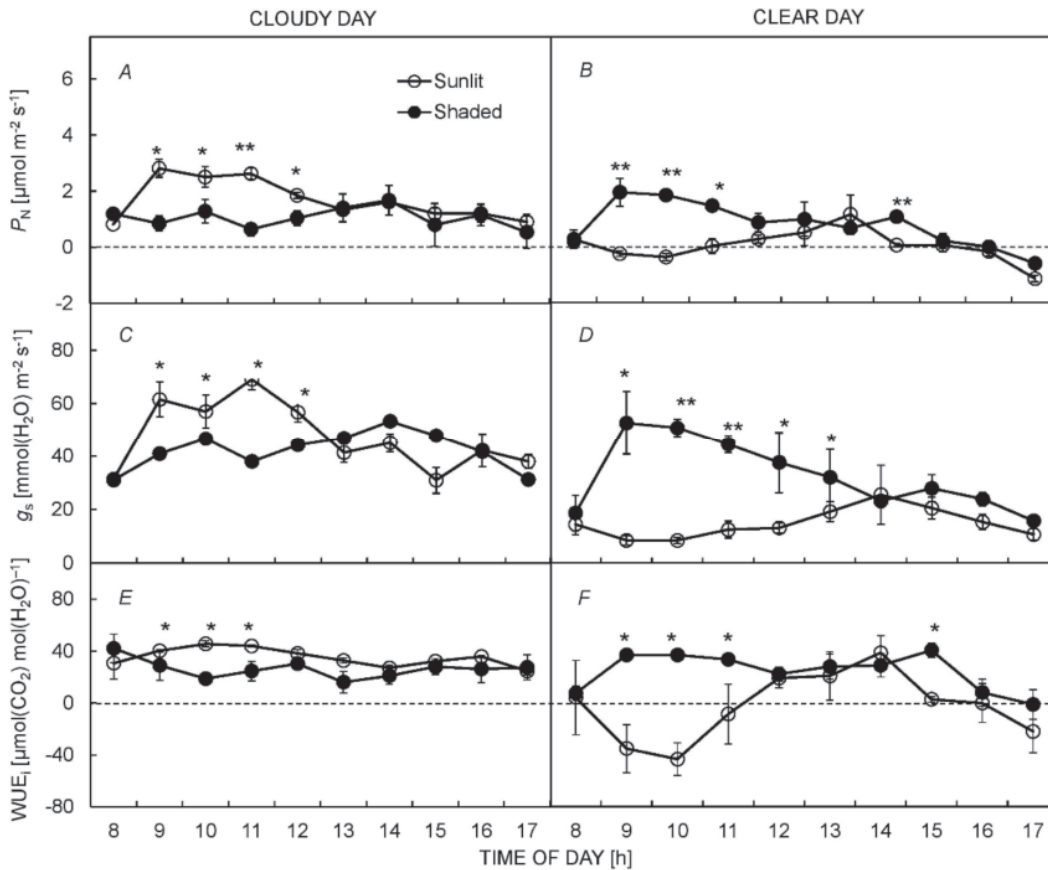
Fig. 3. (*A,B*) Diurnal course of net photosynthetic rate (P_N), (*C,D*) stomatal conductance (g_s), and (*E,F*) intrinsic water-use efficiency (WUE$_i$) of sunlit (O) and shaded leaves (●) of mango measured on the selected cloudy and clear days. *, ** – significant differences between sunlit and shaded at $P \leq 0.05$ and $P \leq 0.01$, respectively. Data are means ± SE, $n = 3$.

Fig. 4. Relationship between stomatal conductance (g_s) and net photosynthetic rate (P_N) of sunlit (O) and shaded leaves (●) measured on a cloudy day (*A*) and a clear day (*B*).

Fruit set and fruit quality: Shading increased the total number of fruits by 23.4%. Fruit mass and fruit sizes were measured at harvesting time. There was no significant difference in fruit mass and fruit size between the two conditions (Table 1). Peel color under natural condition was darker than that under shaded as indicated by lower *L** values (Table 2). TSS and TA contents were not significantly different between sunlit and shaded conditions (Table 2).

Discussion

Mango has a low P_N: it was -23.1 μmol m^{-2} s^{-1} (2−3-day-old leaves), reached the highest value of 9.4 μmol m^{-2} s^{-1} (45-day-old leaves), and subsequently gradually declined with age (Phattarlerphong 1997). The P_N in our experiment showed a low rate and it did not exceed 3.0 μmol m^{-2} s^{-1}, because measurements were taken from old leaves after 135 and 180 d. The first measurements were performed on the cloudy day as defined by the low irradiance with the trees receiving a maximum PPFD of only 1,200 μmol (photon) m^{-2} s^{-1} under natural sunlit conditions and lower than 800 μmol(photon) m^{-2} s^{-1} under the plastic roof (Fig. 2A). The highest P_N value of the sunlit leaves did not exceed 3 μmol m^{-2} s^{-1} until the late morning. Afterwards, a decrease in P_N was observed from midday until late afternoon (Fig. 3A). There was a greater reduction of photosynthesis in the shaded leaves compared to the sunlit leaves on the cloudy day (Fig. 3A). Even during the day, the value of F_v/F_m for both sunlit and shaded leaves did not fall below 0.77 (Fig. 5A), suggesting that photoinhibitory damage to PSII did not occur on the cloudy day. Thus, the reduced P_N for the shaded leaves was due to the lower radiance transmitted through the plastic roof, which may not be suitable for photosynthesis under cloudy conditions. This is strongly supported by the fact that light saturation of photosynthesis in mango cv. Nam Dok Mai has been measured at approximately 600−800 μmol(photon) m^{-2} s^{-1} (Chamchaiyaporn et al. 2013). Low PPFD resulting in limited photosynthesis were also observed in shaded citrus trees (Medina et al. 2002).

Fig. 5. (A,B) Diurnal course of maximum quantum yield of PSII (F_v/F_m), (C,D) photochemical quenching coefficient (q_p), (E,F) nonphotochemical quenching (NPQ), (G,H) electron transport rate (ETR) of sunlit (O) and shaded leaves (●) of mango measured on the selected cloudy and clear days. *, ** – significant differences between sunlit and shaded at $P \leq 0.05$ and $P \leq 0.01$, respectively. Data are means ± SE, $n = 3$.
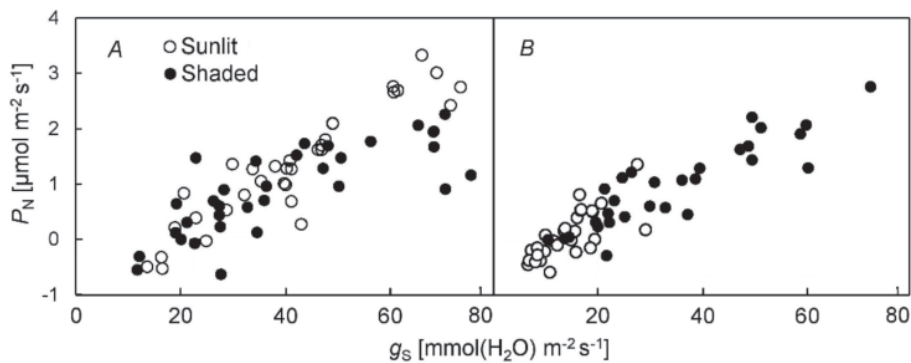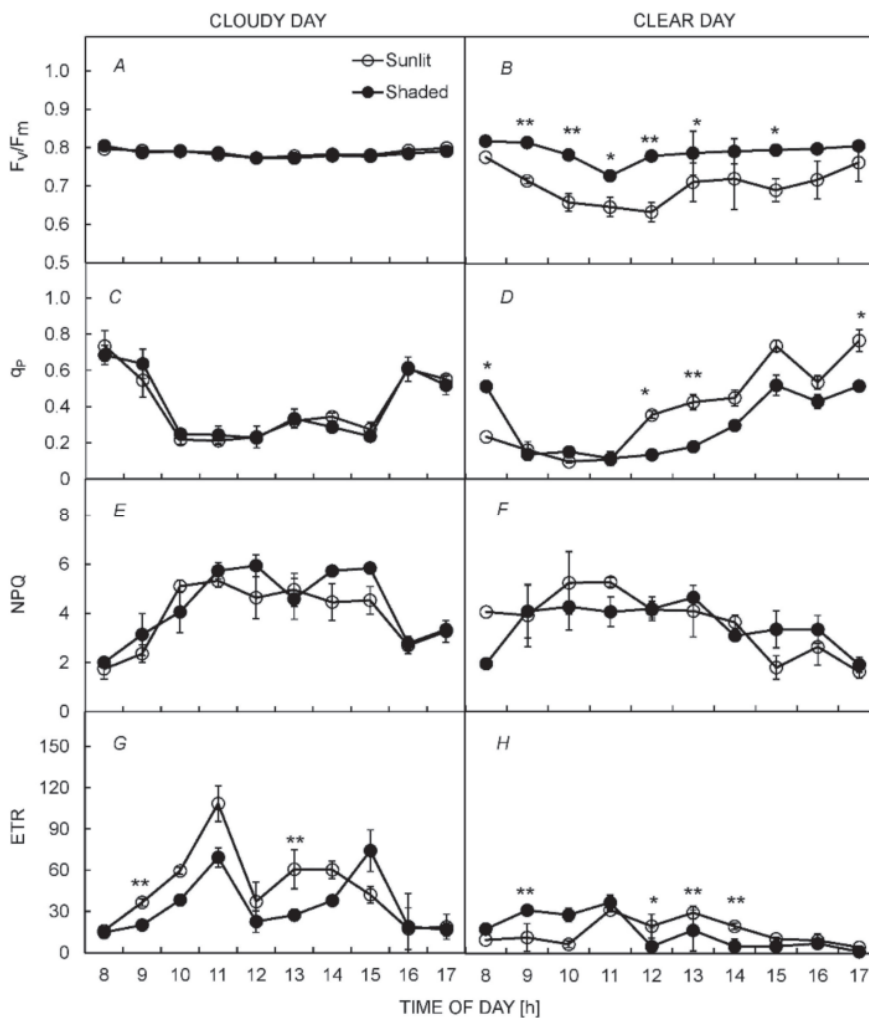
Table 1. Total number of fruit and fruit sizes on mango fruit growth under sunlit and shaded conditions. Data are the means, [A] $n = 10$. [B] $n = 20$.

Treatment	Total number [A] of fruit [number per tree]	Fruit mass [B] [gm]	Fruit size [B] Width [cm]	Length [cm]	Thickness [cm]
Sunlit	155.00	309.22	6.57	15.45	5.98
Shaded	191.30	305.02	6.58	15.37	5.98

Table 2. Peel color, total soluble solid, and titratable acidity of mango fruits grown under sunlit and shaded conditions. * − significant differences between sunlit and shaded at $P \leq 0.05$ by t-test. Each value is the mean, $n = 20$. [A] Peel color characteristics: $L*$ − lightness (black = 0, white = 100), $b*$ − yellow/blue hue component.

Treatment	Peel color [A] $L*$	$b*$	Total soluble solid [Brix]	Titratable acidity [mEq(H$^+$) ml^{-1}]
Sunlit	65.61*	34.85	17.34	0.17
Shaded	67.13	35.96	16.87	0.17

On the clear day, the trees received high PPFD only in the morning (09:00−12:00 h) (Fig. 2B). Large increases in the leaf temperature and VPD$_{leaf-air}$ were observed in the morning to midday measurements (Fig. 2D,F). Increasing of vapour pressure deficit promoting stomatal closure was observed in several species, with a consequent decline in photosynthesis (Monteith 1995, Medina *et al.* 2002, Shirke and Pathre 2004). The gas exchange on the clear day was inhibited and had a lower P_N value in the sunlit leaves than that in the shaded leaves, especially in the morning, when the VPD$_{leaf-air}$ was greater than 2.5 kPa (Figs. 2F, 3B). However, during the experiment, there was no difference between VPD$_{air}$ outside and under the plastic roof while there was a wide variation in VPD$_{leaf-air}$ during the day (Figs. 1D, 2F). Thus, the effect of a high vapour pressure deficit on photosynthesis limitation was considered as a short-term effect. Shade application maintained higher WUE$_i$ (P_N/g_s) in leaves when compared to the sunlit leaves on a clear day (Fig. 3F). This was in accordance with the studies in apricot (Nicolás *et al.* 2005), lemon (Alarcón *et al.* 2006), and citrus (Jifon and Syvertsen 2003). Furthermore, a slight drop of F_V/F_m (0.73) in the shaded leaves was noticed on clear day only at 11:00 h (Fig. 5B). The results indicated that the stomatal limitations of photosynthesis predominated the metabolic limitations with regard to the shaded leaves on a clear day.

There was a lower relationship between P_N and g_s in the sunlit leaves compared to the shaded leaves (Fig. 4B). Furthermore, low g_s values for the sunlit leaves were observed with the high VPD$_{leaf-air}$ (Figs. 2F, 3D). The results indicated that g_s decreased by the increase in VPD$_{leaf-air}$ in the sunlit leaves, with associated high irradiance. Thus, the reduction in P_N of the sunlit leaves was likely modulated partly due to the stomatal limitation.

Excessive irradiance above the light-saturation point may reduce photosynthesis through metabolic impairment (Flexas *et al.* 2004, Montanaro *et al.* 2009, Zhou *et al.* 2010). The analysis of metabolic limitation of

photosynthesis through the WUE$_i$ was used as an indication of the PSII efficiency. In the present study, the WUE$_i$ of the sunlit leave on the clear day decreased during the morning until midday (Fig. 3F) suggesting a non-stomatal limitation of photosynthesis. Furthermore, most research on nonstomatal limitations in tree species reported that high solar energy levels cause a higher degree of photoinhibition (Kamaluddin and Grace 1992, Kitao *et al.* 2000, Tucci *et al.* 2010). Photoinhibition was greater in the sunlit leaves than that in the shaded leaves on the clear day as indicated by the lower F_v/F_m ratio of the sunlit leaves during the morning until midday (Fig. 5B). However, F_v/F_m rapidly recovered in the late afternoon and reached the early morning value. This process is considered a characteristic of dynamic photoinhibition (Einhorn *et al.* 2004), which is the PSII response to avoid damage to the functional integrity of the photosynthetic processes under excessive PPFD. On the other hand, F_v/F_m values on the cloudy day of both shaded and sunlit leaves remained around an optimal value of 0.83 (Björkman and Demmig 1987) throughout the day (Fig. 5A). This indicates that dynamic photoinhibition did not occur on the cloudy day even if the highest on PPFD was 1,100 µmol(photon) m^{-2} s^{-1}. NPQ can represent the energy which cannot be utilized to transport photosynthetic electrons and is dissipated harmlessly as heat energy from PSII light-harvesting complexes (Vasiľev *et al.* 1998, Veres *et al.* 2006). Thus, the large reversible increases in NPQ indicated that thermal energy dissipation occurred and was sufficiently efficient to prevent dynamic photoinhibition under cloudy days.

A decrease in the activity of PSII during the low and high radiance measurements was reflected by the reduction of q$_p$ in both the sunlit and shade leaves at midday (Fig. 5C,D). Since, q$_p$ indicates the proportion of PSII reaction centers that are open (Maxwell and Johnson 2000), high q$_p$ is advantageous for the separation of the electric charge in the reaction center and is beneficial to

electron transport and PSII yield. The results suggested a better light-use efficiency by a higher q_p value in the early morning and late afternoon than that at midday, with a concomitant reduction in the proportion of light destined for heat dissipation (NPQ) (Fig. 5*C,D,E,F*). Hence, the separation of electric charge in the reaction center, the ability to transport electrons, and the quantum yield of PSII of mango trees were weakened from noon until the afternoon. However, the q_p was slightly higher in the sunlit leaves than that of the shaded leaves on the clear day (Fig. 5*F*), suggesting a smaller risk of photoinhibitory damage in the sunlit leaves on the clear day. The ETR value also reveals the relative quantity of electrons passing through PSII during steady-state of photosynthesis (Tezara *et al.* 2003). Exposure to the high irradiance on the clear day in both sunlit and shaded leaves resulted in a greater reduction in the ETR value than on the cloudy day. Reductions in ETR might occur due to the loss of Chl *via* a reduction in the efficiency of excitation capture, most likely from photoinhibition (Flowers *et al.* 2007).

The effect of shade application has been assessed mainly for fruit quality purpose (Snelgar and Hopkirk 1988, Montanaro *et al.* 2006). In the present study, a shade screen was built at the mango blooming stage which means that fruit number was not affected by shading because flower bud had already appeared. However, a higher total fruit number was observed under the shade compared to sunlit conditions. Juntamanee *et al.* (2013) reported that shade screen could reduce damage on mango fruit caused by thrips. Among pests of mango, thrips are especially destructive with regard mango flower inflorescence causing the yield loss (Aliakbarpour and Rawi 2010). Thus, the effect of shade on increasing fruit number might be due to the shading decreasing damage to the mango panicle and reducing the amount of fruits destroyed by thrips. There were no significant effects of shade on the fruit size (Table 1). In most fruit crops, variation of VPD during fruit development impacts on fruit transpiration, xylem water inflow, and calcium accumulation in fruits associated with fruit growth (Montanaro *et al.* 2014). Montanaro *et al.* (2015) also reported that early kiwi fruit development is the most critical period for Ca accumulation and under high VPD conditions, Ca accumulation is coupled to cumulative transpiration. Although, we did not measure fruit transpiration or mineral contents in fruits, we found no difference in VPD_{air} between outside and under the shade roof. Thus, the results suggested that no differentiation in the fruit size might occur due to almost the same VPD_{air} under both conditions, which caused similar transpiration of mango fruit and thus had no effect on water input and fruit growth. Furthermore, the horizontal shade screens increased P_N and decreased photoinhibition on clear day and probably only during the midday hours because the shaded tree canopy could receive direct sunlight in the early morning and late afternoon. This experiment measured photosynthesis performance of leaves on the outside of the canopy, thus the results cannot be extrapolated to other canopy positions or to the whole trees. These reasons might explain why shade had a little effect on the fruit size. Similar results were found in 'Spring' navel orange trees grown under shade screens (Syvertsen *et al.* 2003). Mango fruits from natural conditions exhibited darker peel color as indicated by lower $L*$ values than that of the shaded one (Table 2). There was a report indicating that shading could reduce the anthracnose infection on mango fruit peel at pre- and postharvest periods (Juntamanee *et al.* 2013). Therefore, the reduced area of disease incidence on the mango peel of shaded fruit promoted a more bright coloration compared to fruit from trees growing in the open field.

In conclusion, the reduction of high solar energy caused by the plastic roof resulted in reduced stomatal limitations to carbon supply and mitigated the inactivation of the primary photochemistry associated with PSII. The increase in leaf photosynthesis under shading condition could occur due to shading that lowered the temperature and $VPD_{leaf-air}$; it increased stomatal conductance and the flux of CO_2 into the leaf. Shading also decreased the degree of photoinhibition under full sun light, thereby maintaining higher photosynthetic rate in the shaded leaves than that if the sunlit leaves. Shading increased the total fruit number and shaded fruits showed better skin color development than that of the sun-exposed fruits.

References

Alarcón J.J., Ortuño M.F., Nicolás E. *et al.*: Improving water-use efficiency of young lemon trees by shading with aluminised-plastic nets. – Agr. Water Manage. **82**: 387-398, 2006.

Aliakbarpour H., Rawi C.S.: Diurnal activity of four species of thrips (*Thysanoptera*: *Thripidae*) and efficiencies of three nondestructive sampling techniques for thrips in mango inflorescences. – J. Econ. Entomol. **103**: 631-640, 2010.

Baker N.R., Rosenqvist E.: Application of chlorophyll fluores-cence can improve crop production strategies: an examination of future possibilities. – J. Exp. Bot. **55**: 1607-1621, 2004.

Barron-Gafford G.A., Grieve K.A., Murthy R.: Leaf- and stand-level responses of a forested mesocosm to independent manipulations of temperature and vapour pressure deficit. – New Phytol. **174**: 614-625, 2007.

Björkman O., Demmig B.: Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 k among vascular plants of diverse origins. – Planta **170**: 489-504, 1987.

Chamchaiyaporn T., Jutamanee K., Kasemsap P. *et al.*: Selection of the most appropriate coating particle film for improving photosynthesis in mango. – Kasetsart J. **47**: 323-332, 2013.

Einhorn K.S., Rosenqvist E., Leverenz J.W.: Photoinhibition in seedlings of *fraxinus* and *fagus* under natural light conditions: implications for forest regeneration? – Oecologia **140**: 241-251, 2004.

Flexas J., Bota J., Cifre J. *et al.*: Understanding down-regulation

of photosynthesis under water stress future prospects and searching for physiological tools for irrigation management. – Ann. Appl. Biol. **144**: 273-283, 2004.

Flowers M.D., Fiscus E.L., Burkey K.O. *et al.*: Photosynthesis, chlorophyll fluorescence, and yield of snap bean (*Phaseolus vulgaris L.*) genotypes differing in sensitivity to ozone. – Environ. Exp. Bot. **61**: 190-198, 2007.

Genty B., Briantais J.M., Baker N.R.: The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Goh C.H., Ko S.M., Koh S. *et al.*: Photosynthesis and environments: photoinhibition and repair mechanisms in plants. – J. Plant Biol. **55**: 93-101, 2012.

Goudriaan J., van Laar H.H.: Modelling Potential Crop Growth Processes. Pp. 238. Kluwer Academic Publ., Dordrecht – Boston – London 1994.

Ibrahim M.H., Jaafar H.Z.E.: Photosynthetic capacity, photochemical efficiency and chlorophyll content of three varieties of *Labisia pumila* Benth. exposed to open field and greenhouse growing conditions. – Acta Physiol. Plant. **33**: 2179-2185, 2011.

Jifon J.L., Syvertsen J.P.: Moderate shade can increase net gas exchange and reduce photoinhibition in citrus leaves. – Tree Physiol. **23**: 119-127, 2003.

Juntamanee K., Onnom S., Yingjajaval S. *et al.*: Leave photosynthesis and fruit quality of mango growing under field or plastic roof condition. – Acta Hortic. **975**: 415-420, 2013.

Kamaluddin M., Grace J.: Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. – Ann. Bot.-London **69**: 47-52, 1992.

Kitao M., Lei T.T., Koike T. *et al.*: Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. – Plant Cell Environ. **23**: 81-89, 2000.

Krall J.P., Edwards G.E.: Relationship between photosystem II activity and CO_2 fixation in leaves. – Physiol. Plantarum **86**: 180-187, 1992.

Maxwell K., Johnson G.N.: Chlorophyll fluorescence - a practical guide. – J. Exp. Bot. **51**: 659-668, 2000.

Medina C.L., Souza R.P., Machado E.C. *et al.*: Photosynthetic response of citrus grown under reflective aluminized polypropylene shading nets. – Sci. Hortic.-Amsterdam **96**: 115-125, 2002.

Montanaro G., Dichio B., Lang A. *et al.*: Internal versus external control of calcium nutrition in kiwifruit. – J. Plant Nutr. Soil Sci. **177**: 819-830, 2014.

Montanaro G., Dichio B., Lang A. *et al.*: Fruit calcium accumulation coupled and uncoupled from its transpiration in kiwifruit.

– J. Plant Physiol. **181**: 67-74, 2015.

Montanaro G., Dichio B., Xiloyannis C.: Shade mitigates photoinhibition and enhances water use efficiency in kiwifruit under drought. – Photosynthetica **47**: 363-371, 2009.

Montanaro G., Dichio B., Xiloyannis C., Celano G.: Light influences transpiration and calcium accumulation in fruit of kiwifruit plants (*Actinidia deliciosa* var. deliciosa). – Plant Sci. **170**: 520-527, 2006.

Monteith J.L.: A reinterpretation of stomatal responses to humidity. – Plant Cell Environ. **18**: 357-364, 1995

Nicolás E., Torrecillas A., Dell Amico J., Alarcón J.J.: Sap flow, gas exchange, and hydraulic conductance of young apricot trees growing under a shading net and different water supplies. – J. Plant Physiol. **162**: 439-447, 2005.

Pettigrew W.T., Hesketh J.D., Peters D.B. *et al.*: A vapour pressure deficit effect on crop canopy photosynthesis. – Photosynth. Res. **24**: 27-34, 1990.

Phattarlerphong J.: [Photosynthetic Light Response at Various Leaf Ages in Two Mango Cultivars.] – MSc. Thesis, Kasetsart University, Thailand 1997. [In Thai]

Shirke P.A., Pathre U.V.: Influence of leaf-to-air vapour pressure deficit (VPD) on the biochemistry and physiology of photosynthesis in *Prosopis juliflora*. – J. Exp. Bot. **55**: 2111-2120, 2004.

Snelgar W.P., Hopkirk G.: Effect of overhead shading on yield and fruit-quality of kiwifruit (*Actinidia deliciosa*). – J. Hortic. Sci. **63**: 731-742, 1988

Syvertsen J.P., Goñi C., Otero A.: Fruit load and canopy shading affect leaf characteristics and net gas exchange of 'spring' navel orange trees. – Tree Physiol. **23**: 899-906, 2003.

Tezara W., Martínez D., Rengifo E. *et al.*: Photosynthetic responses of the tropical spiney shrub *Lycium nodosum* (Solanaceae) to drought, soil salinity and salt spray. – Ann. Bot.-London **92**: 757-765, 2003.

Tucci M.L.S, Erismann N.M., Machado E.C. *et al.*: Diurnal and seasonal variation in photosynthesis of peach palms grown under subtropical conditions. – Photosynthetica **48**: 421-429, 2010.

Vasiľev S., Wiebe S., Bruce D.: Non-photochemical quenching of chlorophyll fluorescence in photosynthesis. 5-hydroxy-1, 4-naphthoquinone in spinach thylakoids as a model for antenna based quenching mechanisms. – Biochim. Biophys. Acta **1363**: 147-156, 1998.

Veres S., Tóth V.R. Láposi R. *et al.*: Carotenoid composition and photochemical activity of four sandy grassland species. – Photosynthetica **44**: 255-261, 2006.

Zhou S.B., Liu K., Zhang D. *et al.*: Photosynthetic performance of *Lycoris radiata* var. *radiate* to shade treatments. – Photosynthetica **48**: 241-248, 2010.