

# PHOTOSYNTHESIS IN MEXICAN PLUM [*Spondias purpurea* L. (Anacardiaceae)]

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## SUMMARY

Measurements of diurnal courses in the rates of instantaneous net CO<sub>2</sub> uptake (An) and stomatal conductance (Ce), for *Spondias purpurea* L. were related with photosynthetic photon flux (PPF) and air temperature (TA) in a subtropical environment during the summer of 1998. Leaves of *S. purpurea* L. are thin (137.0 µm), foliar trait regularly associated with canopy environments where light availability is a limiting factor. Total daily PPF in an open field were 49.01 mol·m<sup>-2</sup>·day<sup>-1</sup> in July; 42.12 mol·m<sup>-2</sup>·day<sup>-1</sup> in August, and 16.73 mol·m<sup>-2</sup>·day<sup>-1</sup> in September; however, about 80 % of An measurements were recorded with low levels of instantaneous PPF (<500 µmol·m<sup>-2</sup>·s<sup>-1</sup>), that are below the light saturation point (660 µmol·m<sup>-2</sup>·s<sup>-1</sup>). In spite of the low levels of irradiance, *S. purpurea* L. leaves reached values of An, that range from 10 to 20 µmol·m<sup>-2</sup>·s<sup>-1</sup>. The highest An values were 10.7 µmol·m<sup>-2</sup>·s<sup>-1</sup> in July, 16.2 µmol·m<sup>-2</sup>·s<sup>-1</sup> in August, and 7.5 µmol·m<sup>-2</sup>·s<sup>-1</sup> in September. Daily patterns of net CO<sub>2</sub> uptake showed that An increased during the morning and decreased around noon. The reduction in the rates of An during the day was not related to the reduction of Ce, TA and PPF. The total daily net CO<sub>2</sub> uptake was 359 mmol·m<sup>-2</sup>·day<sup>-1</sup> in July, 646 mmol·m<sup>-2</sup>·day<sup>-1</sup> in August, and 200 mmol·m<sup>-2</sup>·day<sup>-1</sup> in September. An values recorded for *S. purpurea* L. were near the highest values reported for most tropical tree species. Carbon gain might be considered relatively high if we consider that *S. purpurea* L. thrives in infertile stony soils, with a reduced agronomical management.

**ADDITIONAL KEY WORDS:** Net CO<sub>2</sub> uptake rate, stomatal conductance, foliar anatomy, temperature, photosynthetic photon flux, soil moisture content

## FOTOSÍNTESIS EN CIRUELA MEXICANA [*Spondias purpurea* L. (Anacardiaceae)]

## RESUMEN

En un ambiente subtropical se estudió en *Spondias purpurea* L. la variación diurna en las tasas instantáneas de asimilación neta de CO<sub>2</sub> (An) y conductancia estomática (Ce) y su relación con el flujo fotónico fotosintético (PPF) y la temperatura del aire (TA) durante el verano de 1998. Las hojas de *S. purpurea* L. son delgadas (137.0 µm); esta característica foliar está asociada con ambientes con baja disponibilidad de luz. Los valores diarios del PPF en campo abierto fueron 49.01 mol·m<sup>-2</sup>·día<sup>-1</sup> en julio; 42.12 mol·m<sup>-2</sup>·día<sup>-1</sup> en agosto y 16.73 mol·m<sup>-2</sup>·día<sup>-1</sup> en septiembre; sin embargo, 80 % de los valores de An fueron registrados con niveles bajos de PPF (<500 µmol·m<sup>-2</sup>·s<sup>-1</sup>), e inferiores al punto de saturación lumínica (660 µmol·m<sup>-2</sup>·s<sup>-1</sup>). No obstante, en algunas hojas se registraron valores de An que oscilaron de 10 a 20 µmol·m<sup>-2</sup>·s<sup>-1</sup>. Las tasas más altas de An fueron de 10.7 µmol·m<sup>-2</sup>·s<sup>-1</sup> en julio, 16.2 µmol·m<sup>-2</sup>·s<sup>-1</sup> en agosto y 7.5 µmol·m<sup>-2</sup>·s<sup>-1</sup> en septiembre. Los patrones de asimilación neta diaria de CO<sub>2</sub> mostraron que la An se incrementó durante la mañana, disminuyendo al atardecer. No se encontró relación entre la reducción durante el día de la An con Ce, TA y PPF. Los valores de asimilación neta diaria de CO<sub>2</sub> fueron de 359 mmol·m<sup>-2</sup>·día<sup>-1</sup> en julio; 647 mmol·m<sup>-2</sup>·día<sup>-1</sup> en agosto y 200 mmol·m<sup>-2</sup>·día<sup>-1</sup> en septiembre. Los valores de An registrados en *S. purpurea* L. son cercanos a los más altos reportados para árboles tropicales. La ganancia de carbono registrada en *S. purpurea* L. puede ser considerada alta, no obstante que esta especie prospera en suelos pedregosos de baja fertilidad, con un manejo agronómico mínimo.

**PALABRAS CLAVE ADICIONALES:** Tasa de asimilación neta de CO<sub>2</sub>, conductancia estomática, anatomía foliar, temperatura, flujo fotosintético de fotones, contenido de humedad del suelo.

## INTRODUCTION

Since the end of 20<sup>th</sup> century Mexican horticulturists have paid special attention to native fruit crops from tropical and subtropical regions of Mexico, mainly because most of them are considered to be exotic fruit in the international markets. They yield high prices compared with other tradi-

tional fruit crops. The Mexican plum (*Spondias purpurea* L.) is useful for the reforestation of degraded lands, because it thrives satisfactorily in infertile rocky soils, and produces edible marketable fruits that ripen in the spring, when few fresh fruits are available to consumers in the local markets (Pennington and Sarukhan, 1998; Vázquez-Yanes *et al.*, 1999, Macia and Barfod, 2000). The use of the fruits of

*Spondias* in Mexico dates back to prehispanic cultures (Díaz del Castillo, 1992), when the fruits were gathered from wild populations that grew as a part of the low deciduous forest (Turner and Miksicek, 1984; De Acosta, 1985; Benitez 1986; Rzedowski, 1994). At the present time, both wild and cultivated populations of *S. purpurea* L. are common in the deciduous forests along the west coast of Mexico, from Sonora to Chiapas (Pennington and Sarukhan, 1998), and other related species are cultivated worldwide in different subtropical and tropical regions (Campbell, 1996; Pennington and Sarukhán, 1998; Macia and Barfod, 2000). In central western Mexico, *S. purpurea* L. was one of the most important fruit crops at the end of the 19<sup>th</sup> century (Aldana, 1986). Recently fruit demands of *S. purpurea* L. have increased for both their consumption as a fresh fruit, and for processing to obtain beverages, marmalades and honeys, among other products (Cuevas, 1994). Nevertheless, the successful establishment and management of *S. purpurea* L. in land reclamation projects are limited by the lack of knowledge concerning ecophysiological aspects of *S. purpurea* L. (Vázquez-Yanes *et al.*, 1999). The understanding of the effects of environmental factors on photosynthesis of *S. purpurea* L. trees, might help to improve its management as a fruit crop or forest tree, and for the ecological understanding also of aspects related to the cycles of carbon and of the water in these ecosystems (Bassoz and Bazzaz, 1998).

Because information in ecophysiological aspects of *S. purpurea* L. is scarce (Vázquez-Yanes *et al.*, 1999) the main objective of this work was to relate the effects of daily microclimatical variations in temperature and light during the summer months on the gas exchange of mature trees of *S. purpurea* L.

## MATERIALS AND METHODS

Mexican plum (*Spondias purpurea* L.) belongs the family Anacardiaceae, tribe Spondiadeae, which comprise 17 genera. *Spondias* is one of the most important genera of the tribe and is native of the deciduous forests of tropical and subtropical environments of Mexico and Central America; *S. purpurea* L. is a deciduous tree that grows to 12 m of high, with a well defined trunk, with numerous branches (Pennington and Sarukhan, 1998; Macia and Barfod, 2000). Flowering started early January, ending in early February. Fruit development started at the middle of February, and fruit ripening started late March, ending early June. The fruit is a small drupe, whose form varies of elliptic to ellipsoidal. The common colors of epicarp are yellow and red; the pericarp is juicy, with sweet to bittersweet flavor (Castro, 1977; Avitia, 1996). The cultivated trees grow in rocky soils with medium slope, and lower fertility soil (Castro, 1977), and are classified as regosol, with a pH slightly alkaline (Galván, 1988; Rzedowski, 1994). The climate in the study site is classified like subtropical sub-humid (Medina-García *et al.*, 1998).

This physiological and microclimatical observations were realized during the summer of 1998, in three dates: July 29, August 28, and September 30 in a cultivated population of *S. purpurea* L. located in San Francisco de Ixcatan, Municipality of Zapopan, Jalisco, located at 103°19'42" W and 20°50'29" N. Soil water content was determined for 10 soil samples removed from the rizosphere (a depth of 15 cm), in different places of the plantation. Soils were dried at 80 °C to constant mass (generally within 72 h); data are expressed as percentage water content: (fresh mass – dry mass)/ fresh mass x 100 (Torres, 1984). Photosynthetic photon flux (PPF; wavelengths of 400 to 700 nm) was measured hourly from sunrise to sunset with a LI-190S quantum sensor (LICOR, Lincoln, Nebraska), in open field with full exposition to the light and in different canopy positions, each time that the measurements were carried out of uptake net of CO<sub>2</sub> (An). The air temperature (TA) was recorded each hour with a mercury thermometer.

For anatomical study mature leaves were collected from different canopy positions and fixed in formalin: acetic acid: ethanol (10:5:85) (FAA). Leaf transversal sections (approximately 120 µm) were cuts with a shave knife, and then stained with aniline blue 0.5 % (w:w). Leaf thickness of stomatal frequency was determined using epidermal prints of colorless nail polish. The anatomical observations were realized using a compound Carl Zeiss microscope (Oberkochen, Germany).

Net CO<sub>2</sub> uptake (An), and stomatal conductance (Ce) were measured each two hours during the day from sunrise to sunset, choosing randomly leaves in different canopy positions in 20 mature 25 years old trees of *S. purpurea* in the plantation with a Li-Cor LI-6200 portable photosynthesis system equipped with a 0.25 liter chamber (Li-Cor, Lincoln, NE).

The individual measurements of An were grouped in four ranks of PPF (0-500, 501-1000, 1001-1500, and 1501-2000 µmol·m<sup>-2</sup>·s<sup>-1</sup>), to relate the variation of PPF with An values. The values of An, Ce, PPF and TA were used to elaborate graphics of the diurnal variation.

Analysis of variance was performed on the soil water content, Ta, total daily PPF, An, Ce for the different months under study. Standard error values were calculated also for An, Ce, PPF, and Ta for each time of measurements during the diurnal measurements of gas exchange (Little and Hills, 1987).

## RESULTS AND DISCUSSION

The leaves of *S. purpurea* L. are bifacial, with a dorsal surface of palisade parenchyma, and a well developed spongy parenchyma on the ventral side. Leaves are thin (137.0 µm), with an stomatal density considered high (505 per mm<sup>2</sup>), compared with deciduous fruit trees of temper-

ate climate (Ryugo, 1988; Larcher, 1995), but similar to values reported for tropical trees (Bolh ar-Nordenkampf and Draxler, 1993; R ocas *et al.*, 1997). Their foliar anatomy presents a resemblance to species with C<sub>3</sub> metabolism (Mauseth, 1988; Salisbury and Ross, 1992; Larcher, 1995), which is supported by the fact the majority of the trees that grow in subtropical and tropical climates are considered to have C<sub>3</sub> metabolism (Salisbury and Ross, 1992; Lambers *et al.*, 1998; Sage, 2001). Thin leaves regularly are associated with canopy environments where light availability is considered to be one of the most important environmental factors that influences growth and survival in tropical forest (Chazdon *et al.*, 1996; Strauss-Debenedetti and Bazzaz, 1996). Thin leaves also reflect a low investment of energy for both construction and maintenance (Kozlowski *et al.*, 1991; Ellsworth and Reich, 1993; Strauss-Debenedetti and Bazzaz, 1996; Barnes *et al.*, 1998).

Most of the trees growing in the subtropical study site, as is the case of *S. purpurea* L., produce short-lived deciduous leaves, and drops leaves at the end of the summer rainfall season. Leaf abscission at the beginning of the dry season is considered an avoidance mechanism to water scarcity (Chazdon *et al.*, 1996; Goldstein *et al.*, 1996; Mulkey and Wright, 1996). Many species of plants that grow in low-nutrient environments produced long-lived evergreen leaves because there are insufficient nutrients to support rapid leaf turnover (Chapin III, 1980). Paradoxically *S. purpurea* L. produce short-lived deciduous leaves even though it commonly grows in infertile rocky environments, nevertheless, their leaves show a relatively high photosynthetic activity, as occurs in most deciduous plants that produce short-lived leaves. High photosynthetic activity allows larger carbon gain per unit of biomass invested in leaves (Tivy, 1993; Chapin III *et al.*, 2002).

Total daily PPF in an open field was highest at the beginning of summer (July), decreasing gradually through the summer (August and September) (Table 1), paralleling the gradual increase in cloudiness and relative air humidity observed during the study period. As a consequence, the internal zones of the canopy received 27.5 % of the total daily PPF in July, 35 % in August, and 43 % in September (Table 1). The gradual increase in cloudiness during the summer also affected air temperature, since daily average values decreased gradually during the summer (Table 1). Daily PPF levels within the canopies of *S. purpurea* L. commonly varied from 10 to 700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , although on the periphery of the exposed foliage or an open sites PPF values reached values near 2000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  during the measurement months (Figures 2, 3 and 4). An rates were close to or above values recorded for deciduous trees in other tropical environments, notwithstanding the relatively low levels of light that reach the foliage of *S. purpurea* L. (Strauss-Debenedetti and Bazzaz, 1996; Huante and Rinc n, 1998) and deciduous trees in a temperate environment (Ellsworth and Reich, 1993).

TABLE 1. Mean soil water content (SWC), air diurnal temperature (DT), total daily photosynthetic photon flux (TPPF) in an open field and within the canopy for *Spondias purpurea* L., at San Francisco de Ixcatan, Zapopan, Jalisco. Summer 1998.

Dates of Measurement (1998)	SWC (%)	DT (�C)	TPPF in an Open Field ( $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ )	TPPF Within the Canopy ( $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ )
July 28	22.2 a <sup>z</sup>	29.3 a	49.01 a	13.5 a
August 29	25.1 a	27.7 b	42.12 a	14.64 a
September 30	15.4 b	25.8 c	16.73 b	7.26 b

<sup>z</sup>Means followed by the same letter are not statistically different according to the Tukey's test at a  $P\leq 0.05$

Approximately 80 % of An measurements were recorded with values of PPF lower to 500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Figure 1), values that are below the light saturation point (660  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). In fact, the range of light saturation point from tropical trees varies from 450-600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Wright 1996). These values correspond to one fourth of the maximum PPF that reaches the foliage in an open site ( $\geq 2000$   $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). This situation is common in tree canopies, since the majority of the leaves receive light intensities lower than the light saturation point (Stephen *et al.*, 1996; Gonz lez-Rodr guez *et al.*, 2001).

Most of the studies on photosynthesis rely merely upon instantaneous rates of net CO<sub>2</sub> uptake (Nobel, 1991). Few authors report total daily assimilation values or diel patterns of carbon gain (24 h) in deciduous and evergreen trees (Ellsworth and Reich, 1993; Kozlowski *et al.*, 1991; Zotz and Winter, 1996), or annual C<sub>3</sub> and C<sub>4</sub> plants (Nobel, 1991). Data on total daily carbon gain are more valuable for estimating photosynthetic productivity than instantaneous rates of net CO<sub>2</sub> uptake (Nobel, 1991). In this study we estimated daily net CO<sub>2</sub> uptake by integrating the instantaneous rates during the day and subtracting from this value 15 % of the diurnal carbon gain, considering that 15 % represents an average of carbon loss during dark respiration (Nobel, 1991; Salisbury and Ross, 1992). Therefore, daily carbon gains were 359  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  in July; 646  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  in August, and 200  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  in September (Table 2). The values registered in July, August and September were of 35, 63 and 19 % with respect to the highest values of daily net CO<sub>2</sub> assimilation for C<sub>3</sub> plants (i.e. *Medicago sativa* L.), and 28, 51 and 15 % for C<sub>4</sub> plants (i.e. *Amaranthus palmeri* S. Wats.) (Nobel, 1991). Carbon gain for *S. purpurea* L. might be significant because trees grow on rocky slopes, in shallow infertile soils and with a minimum of management from growers.

Diurnal depression of An for *S. purpurea* L. leaves was observed early morning in July, late afternoon in August, and at the end of the day in September (Figures 2a; 3a; 4a). Depression of An during the day is common in temperate woody forests (Bazzaz, 1996; Bassow and Bazzaz, 1998), temper-

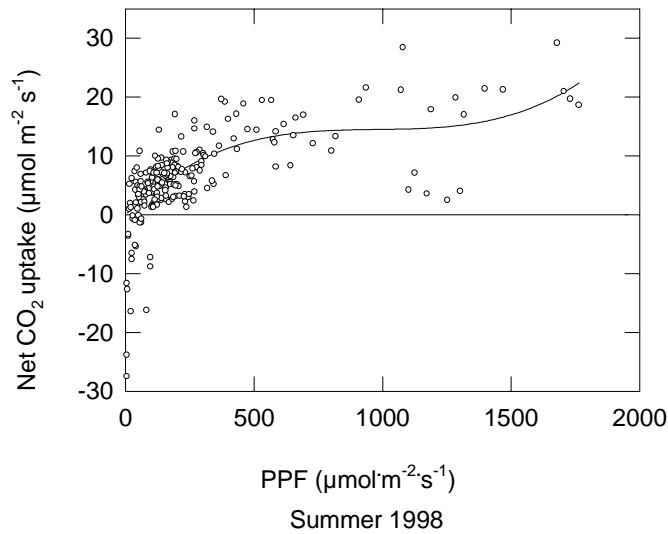


Figure 1. Scatter diagram of net CO<sub>2</sub> uptake for *Spondias purpurea* L., versus photosynthetic photon flux (PPF) at the time of measurement at San Francisco de Ixcatan, Jalisco, México, Summer 1998 (n=224).

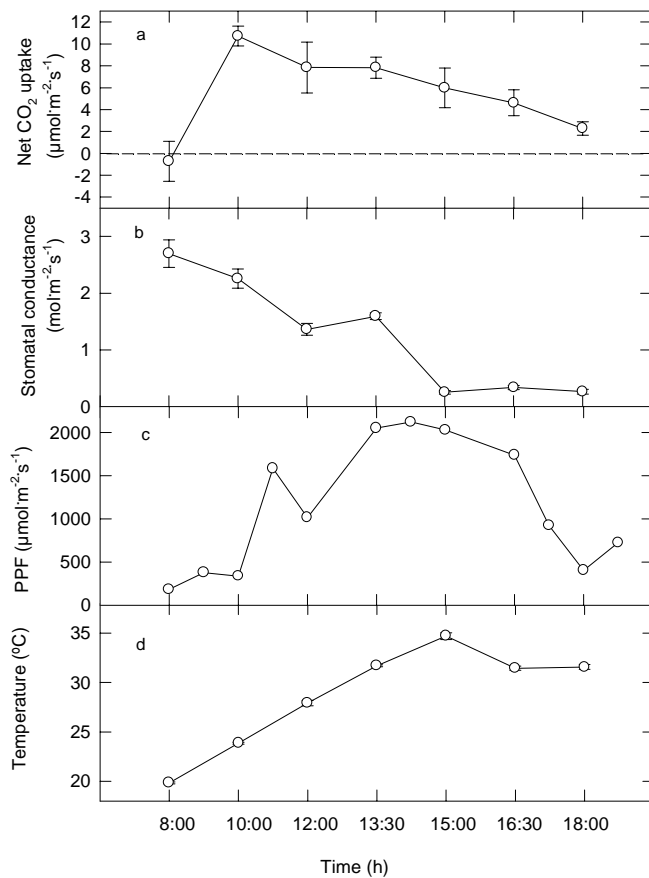


Figure 2. Diurnal variation of net CO<sub>2</sub> uptake (a), stomatal conductance (b) photosynthetic photon flux (PPF) (c), and air temperature (d), for Mexican plum (*Spondias purpurea* L.) at San Francisco de Ixcatan, Jalisco, July 1998. Each point  $\pm$  standard error.

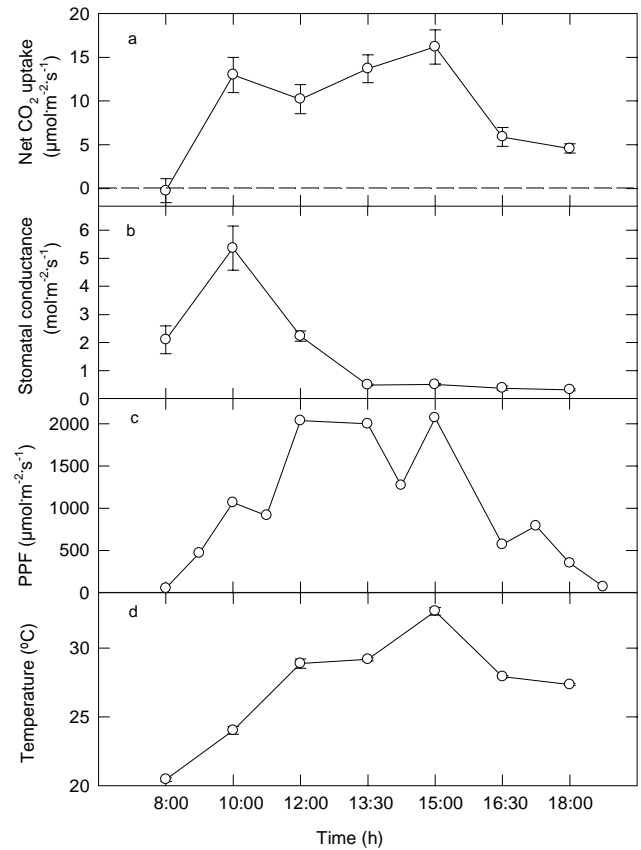
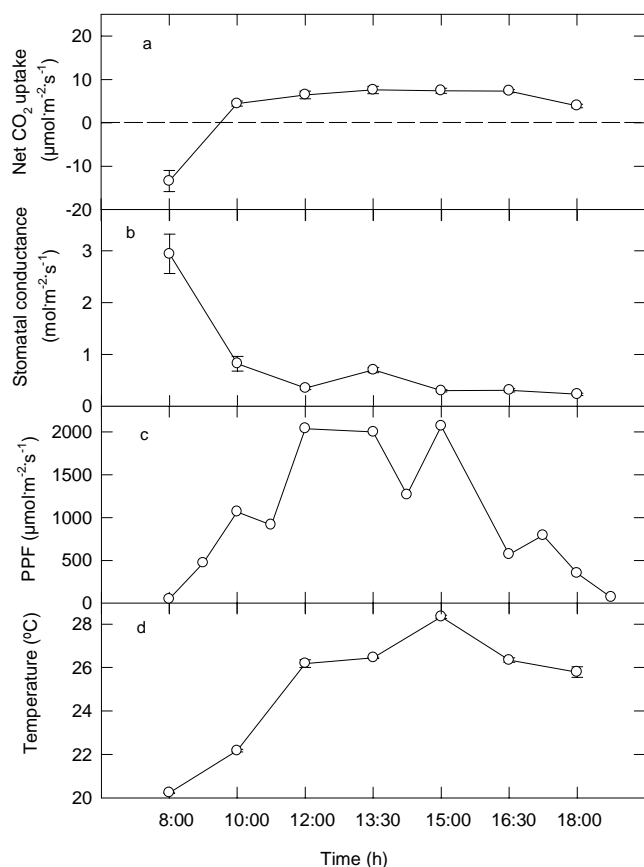


Figure 3. Diurnal variation of net CO<sub>2</sub> uptake (a), stomatal conductance (b) photosynthetic photon flux (PPF) (c), and air temperature (d), for Mexican plum (*Spondias purpurea* L.) at San Francisco de Ixcatan, Jalisco, August 1998. Each point  $\pm$  standard error.

ate fruit crops (Matos *et al.*, 1998), and in subtropical fruit crops (Marler *et al.*, 1994; Greer, 1998), regularly occurring around noon attributed to high temperatures (Sinclair and Allen, 1982; Cowan, 1995; Matos *et al.*, 1998), drought (Larcher, 1995) and high PPF levels (Marler *et al.*, 1994; Pathre *et al.*, 1998). These cause photoinhibition (Mohotti and Lawlor, 2002), and stomatal closure (Sinclair and Allen, 1982). However, early morning depression in July for *S. purpurea* L. does not agree with high levels of PPF and TA (Figure 2), and in August depression occurs after noon, matching both high levels of PPF (2,000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and TA (>33 °C). Nevertheless, lower values of An registered in September are attributed to low light availability because of cloudiness (Table 1), and because the leaves were initiating senescence, which reduces Ce and An (Figure 4) (Yodder *et al.*, 1996; Bassow and Bazzaz, 1998). Moreover drought might not be an important environmental factor involved in An depression during the measurements in *S. purpurea* L., because soil water content was above field capacity (Table 1).

We consider that other factors might be involved in An depression during the day. For instance recent work revealed that the maximal content of starch for *S. purpurea* L. occurred after the maximal peak of net CO<sub>2</sub> uptake



**Figure 4.** Diurnal variation of net CO<sub>2</sub> uptake (a), stomatal conductance (b) photosynthetic photon flux (PPF) (c), and air temperature (d), for Mexican plum (*Spondias purpurea* L.) at San Francisco de Ixcátán, Jalisco, September 1998. Each point  $\pm$  standard error.

(Pimienta-Barrios and Ramírez-Hernández, 2003). Indeed, feedback inhibition by starch (Nakano *et al.*, 1997) may help to account for the decreased the rate of net CO<sub>2</sub> uptake during the day. Photorespiration is considered one of the main causes of the reduction of An values in C<sub>3</sub> plants such as *S. purpurea* L. Regularly both high temperatures and high levels of PPF commonly enhance photorespiration, because it increases the activity of Rubisco as an oxygenase and reduces carboxylation activity (Maxwell *et al.*, 1997). Indeed, temperatures above 30 °C were recorded for July and August and near 30 °C for September, and maximal PPF values varied from 1600 to 2100  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Figures 2, 3 and 4).

Regularly high TA reduces Ce values, affecting An. However, the daily Ce variation patterns during the measurement months did not show a clear relation with An. For instance in July Ce values tended to decrease through the day paralleling the decrease in the rates of An (Figure 2), but a decrease of Ce during the day was not accompanied by a parallel decrease in An in August (Figure 3) and in September (Figure 4). In contrast, the daily patterns of Ce variation were more closely related to changes in TA dur-

ing the measurement months (Figures 2, 3 and 4). Nevertheless, the average daily Ce values during the day proved to be statistically superior in August, than in July and September. So the highest values of stomatal opening coincided with the month that presented the highest values of carbon gain during the day (Table 2).

**TABLE 2.** Instantaneous rates of CO<sub>2</sub> uptake, daily net CO<sub>2</sub> uptake and average daily of stomatal conductance in for *Spondias purpurea* L., at San Francisco de Ixcátán, Zapopan, Jalisco.

Dates of Measurements (1998)	Instantaneous Rates of CO <sub>2</sub> Uptake (mmol·m <sup>-2</sup> ·s <sup>-1</sup> )	Daily Net CO <sub>2</sub> Uptake (mmol·m <sup>-2</sup> ·day <sup>-1</sup> )	Daily Average of Stomatal Conductance (mol·m <sup>-2</sup> ·day <sup>-1</sup> )
July 28	10.7 b <sup>z</sup>	359 b	1.05 b
August 29	16.2 a	646 a	1.72 a
September 30	7.6 b	200 b	0.76 b

<sup>z</sup>Means followed by the same letter within columns are not different according to the Tukey's test at a  $P\leq 0.05$

## CONCLUSIONS

Carbon gain in *S. purpurea* L. might be significant compared with other trees, because trees for *S. purpurea* L. grow in rocky slopes and shallow infertile soils, and with a minimum of management from growers. No clear evidence was found indicating that environmental factors such as light, air temperature or soil moisture participate in the regulation of carbon gain for *S. purpurea* L. Other factors such as feedback inhibition by starch and photorespiration may be involved in the regulation of photosynthesis.

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