TEMPERATURE RESPONSE OF PHOTOSYNTHESIS AND ITS INTERACTION WITH LIGHT INTENSITY IN SWEET ORANGE LEAF DISCS UNDER NON-PHOTORESPIRATORY CONDITION

Resposta da fotossíntese à temperatura e sua interação com a intensidade luminosa em discos foliares de laranjeira doce na ausência de fotorrespiração

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ABSTRACT

This study aimed to evaluate the response of photosynthesis (*A*), given by photosynthetic O_2 evolution, to increasing temperature from 25 to 50ºC in sweet orange (*Citrus sinensis* (L.) Osbeck) leaf discs under non-photorespiring conditions. In order to evaluate the response of gross photosynthesis to temperature and the balance between photosynthetic and respiratory activities, respiration (R_d) rates were also measured, i.e. the O_2 uptake in each temperature. In addition, light response curves of photosynthesis were performed by varying the photosynthetic photon flux density (*PPFD*) from 0 to 1160 μ mol m^{-2} s^{-1} at 25 and 40ºC. The highest *A* values were observed at 35 and 40ºC, whereas the highest R_d values were noticed at 50ºC. A higher relationship A/R_d was found at 30 and 35ºC, suggesting an optimum temperature of 35ºC when considering the balance between photosynthesis and respiration under non-photorespiring condition. Overall, heat effects on plant metabolism were more evident when evaluating the relationship A/R_d. In light response curves, higher *A* values were also found at 40ºC under *PPFD* higher than 300 μ mol m^{-2} s^{-1}. Light saturation point of photosynthesis was increased at 40ºC, without significant change of quantum efficiency under low *PPFD*. Respiration was also enhanced at 40ºC, and as a consequence, the light compensation point increased. The better photosynthetic performance at 35-40ºC was supported by higher photochemical efficiency in both light and temperature response curves. The temperature-dependence of photosynthesis was affected by growth temperature, i.e. a high air temperature during plant growth is a probable factor leading to a higher photosynthetic tolerance to heat stress.

Index terms: *Citrus sinensis*, heat stress, high temperature, O_2 evolution.

RESUMO

Este estudo foi conduzido para avaliar a resposta da fotossíntese (*A*), dada pela evolução fotossintética de O_2, ao aumento da temperatura de 25 para 50ºC em discos foliares de laranjeira doce (*Citrus sinensis* (L.) Osbeck) sob condição de não-fotorrespiração. Visando avaliar a resposta da fotossíntese bruta à temperatura e o balanço entre as atividades fotossintética e respiratória, a taxa de respiração (R_d) foi também medida, i.e. a absorção de O_2 em cada temperatura. Avaliaram-se ainda, as curvas de resposta da fotossíntese à luz, variando-se a densidade de fluxo de fótons fotossintéticos (*DFFF*) entre 0 e 1160 μ mol m^{-2} s^{-1}, a 25 e 40ºC. Maior fotossíntese líquida (*A*) foi observada a 35 e 40ºC, ao passo que os maiores valores de R_d foram verificados a 50ºC. Uma alta relação A/R_d foi verificada a 30 e 35ºC, sugerindo a temperatura ótima de 35ºC quando considerado o balanço entre fotossíntese e respiração sob condição de não-fotorrespiração. Os efeitos da temperatura no metabolismo vegetal foram mais evidentes quando avaliada a relação A/R_d. Nas curvas de resposta à luz, maiores valores de *A* também foram observados a 40ºC em *DFFF* superior a 300 μ mol m^{-2} s^{-1}. O ponto de saturação luminosa da fotossíntese foi aumentado a 40ºC, sem alterações significativas na eficiência quântica sob baixa *DFFF*. A respiração também foi estimulada a 40ºC, e como conseqüência, houve aumento do ponto de compensação luminoso. O melhor desempenho fotossintético a 35-40ºC foi relacionado com uma maior eficiência fotoquímica, tanto na curva de resposta à temperatura como à luz. A dependência da fotossíntese em relação à temperatura foi afetada pela temperatura de crescimento, i.e. maior temperatura do ar durante o crescimento das plantas é um provável fator determinante da maior tolerância fotossintética ao estresse térmico.

Termos de indexação: Alta temperatura, *Citrus sinensis*, estresse térmico, evolução de O_2.

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INTRODUCTION

Temperature is one of the most important environmental factors that influence plant physiology, being the photosynthetic activity especially sensitive to stresses caused by unfavorable temperatures (BERRY & BJÖRKMAN, 1980; BJÖRKMAN et al., 1980; GEORGIEVA, 1999). It is well-known that photosynthesis determines plant growth and development by incorporating atmospheric carbon into carbohydrates. The effects of both instantaneous and growth temperatures on photosynthetic

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machinery have attracted attention of plant physiologists who are interested in studying the physiological responses of citrus plants to temperature changes (KHAIRI & HALL, 1976; RIBEIRO et al., 2003, 2004).

Temperature effects on photosynthesis may occur through an increased oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (BERRY & BJÖRKMAN, 1980; LAISK et al., 1998; RIBEIRO et al., 2004) as well as impaired photochemical activity due to membrane injury and damage of electron transport chain components (BERRY & BJÖRKMAN, 1980). In addition to the inhibition of Rubisco activase (LAW & CRAFTS-BRANDNER, 1999), high temperature may also limit photosynthesis by stomatal closure under photorespiring condition (RIBEIRO et al., 2004).

Some studies have been focused on the response of sweet orange plants to temperature (RIBEIRO et al., 2003, 2004) due to their economical importance in Brazil, a well worldwide known producer and supplier of both orange fruit 'in natura' and its derivatives. Furthermore, the importance of studying the response of citrus photosynthesis to temperature is increased due to (i) the climatic diversity among citrus growing areas in Brazil, especially in the São Paulo State where citrus orchards are distributed in areas with distinct environmental characteristics ranging from climates Aw (in Western and Northern regions, characterized by dry winter and wet summer) to Cfa (in Central region, characterized by a dry season and mean air temperature higher than 22ºC in the hottest month) according to the Köppen classification (PEREIRA et al., 2002; ROLIM et al., 2005); and (ii) the current biotic pressure caused by the attack of some pests and diseases and their relationship with environmental conditions (RIBEIRO et al., 2004), leading to differential productivity response of citrus orchards depending on geographic region and climate.

This study aimed to evaluate the response of the photosynthetic O_2 evolution to increasing temperature in sweet orange [*Citrus sinensis* (L.) Osbeck] leaf discs under non-photorespiratory conditions, considering respiratory changes and the interaction of temperature with light intensity.

MATERIAL AND METHODS

Leaf discs (10 cm^2) were excised from fully expanded and exposed leaves of sweet orange plants [*Citrus sinensis* (L.) Osbeck *cv.* Pêra] grown in pots filled with a mixture of soil, sand, and cow dung (2:1:1, w/w), and supplemented with NPK. Plants were grown under greenhouse or nursery conditions, irrigated and fertilized periodically. Under greenhouse condition, plants were submitted to a warmer environment caused by the plastic cover. The maximum and minimum air temperatures were 42 and 18ºC under greenhouse condition and 34.6 and 6.9ºC under nursery condition, respectively. The greenhouse was located between builds, and had concrete ground cover, which increased air temperature especially during midday. Increases in air temperature have been well documented inside greenhouses with plastic cover (FARIAS et al., 1993).

Photosynthetic rates (*A*, μmol m^{-2} s^{-1}) were measured with a Clark-type electrode, using the LD2/3 leaf chamber (Hansatech, King's Lynn, Norfolk, UK). Data were recorded using the software Oxygraph measurement system v.2.22 (Hansatech) after photosynthesis induction, as indicated by the linear change in the photosynthetic O_2 evolution. Measurements were performed under air CO_2 saturation promoted by 2 mL of a carbonate/bicarbonate buffer solution (1 M, 1:19 v/v), which induces a CO_2 concentration around 2.9% inside leaf chamber. Under such situation, the photorespiration is expected to be abolished; furthermore it is possible to analyze the photosynthetic performance without stomatal limitations (DELIEU & WALKER, 1981; WALKER, 1990).

Photosynthetic photon flux density (*PPFD*) incidence on leaf disc was controlled using optical filters and varying the voltage supplying to the LS3 light source (Hansatech). *PPFD* was fixed in 1160 μmol m^{-2} s^{-1} for evaluating the photosynthetic O_2 evolution in response to increasing temperature (from 25 to 50ºC in steps of 5ºC). Temperature control was provided by using a water bath model MA-127 (Marconi, Piracicaba, SP, Brazil) and leaf temperature was monitored with a copper-constantan thermocouple (AWG 24, Omega Eng., Stamford, CT, USA) attached to the abaxial surface of the leaf disc. Temperature response curves were evaluated in leaf discs of plants grown under greenhouse or nursery conditions.

Light response curves of photosynthesis were studied by varying *PPFD* between 0 and 1160 μmol m^{-2} s^{-1} at 25 and 40ºC. The instantaneous quantum efficiency of photosynthesis [a_I, mmol O_2 (μmol photon$)^{-1}$] was calculated in each *PPFD* as $\alpha_I = [A/(PPFD \times 0.84)]$, where 0.84 is adopted as the fraction of light absorbed by leaves (DEMMIG & BJÖRKMAN, 1987). From light response curves, we derived the following parameters: maximum photosynthetic rate (A_{max}); overall quantum efficiency (α_O), given by the initial linear slope; light saturation point ($PPFD_S$); and light compensation point ($PPFD_C$). Light response curves were evaluated in leaf discs of plants grown under greenhouse conditions.

Dark respiration (R_d, μ mol m^{-2} s^{-1}) was assessed before illuminating leaf discs in light response curves and in each step of temperature response curve for plants growing under greenhouse conditions. Leaf discs were submitted to increasing temperature under dark condition to avoid the stabilizing effect of light on the photosystems (HAVAUX et al., 1991; KALITUHO et al., 2003). As performed in light measurements, values of R_d were only recorded when a constant linear change (steady state) in leaf O_2 uptake was observed. In addition, the gross photosynthesis was assessed as the sum of net photosynthesis (*A*) and respiration (R_d).

In temperature response curves, the same leaf disc was used in measurements of photosynthesis and respiration, being leaf discs maintained during 40 min. in each temperature (30 min. for dark-adaptation and measurement of R_d, and other 10 min. for photosynthesis induction at 125 μ mol m^{-2} s^{-1} and subsequent photosynthesis measurement at varying light intensities, depending on the response curve) under 2.9% CO_2. In light response curves, dark-adaptation and photosynthesis induction at 25 and 40ºC were similar to temperature response curves, and measurements of photosynthesis were taken in each *PPFD* level when photosynthetic O_2 evolution reached steady state (about 4 min. after setting each *PPFD* level).

Data were submitted to ANOVA procedure and means were compared by the Tukey test (at 0.05 probability level) when statistical significance was detected, i.e. mean values of each light level or temperature were compared in both light and temperature response curves.

RESULTS AND DISCUSSION

The photosynthetic O_2 evolution showed an increasing trend up to 40ºC, when decreases were probably caused by heat stress (Fig. 1A). Such a trend was accompanied by the quantum efficiency of photosynthesis (Fig. 1C), suggesting similar heat lability between photosynthetic O_2 evolution and photochemical activity.

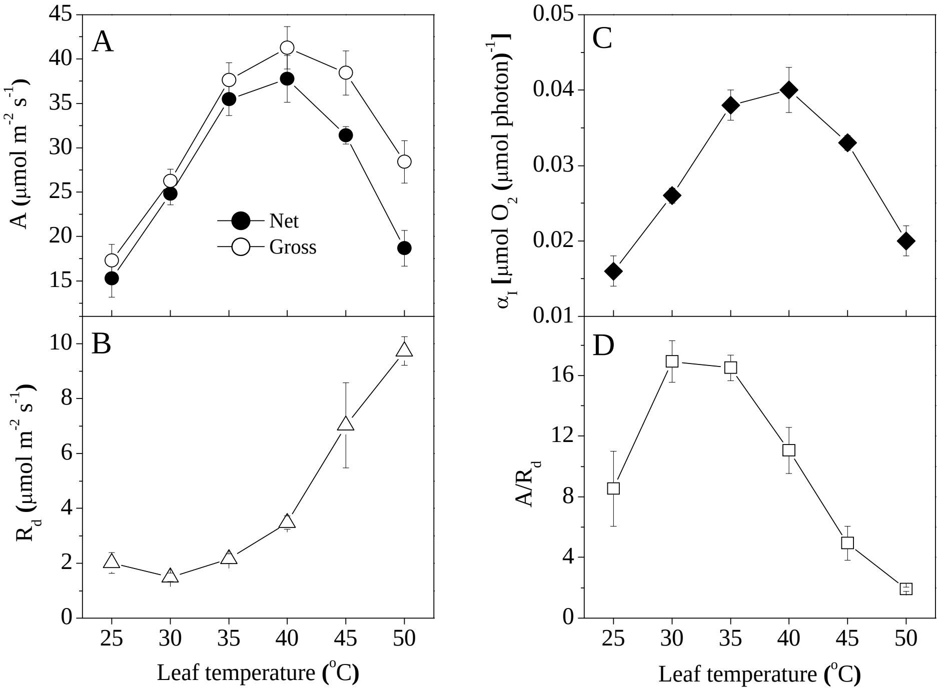

FIGURE 1 – Net and gross photosynthesis (*A*, A), dark respiration (R_d, B), instantaneous quantum efficiency of photosynthesis (α_I, C) and relationship between photosynthesis and respiration (A/R_d, D) as a function of leaf temperature in sweet orange leaf discs under non-photorespiratory condition. Gross photosynthesis refers to the sum of net photosynthesis and respiration. Each point represents the mean value (n=5) ± SE. Leaf discs were excised from plants grown under greenhouse conditions.

It is known that optimum temperature for leaf photosynthesis in citrus plants is between 20 and 30ºC under humid conditions (KRIEDEMANN, 1968; RIBEIRO et al., 2004), however, this optimum temperature shifts under CO_2-saturated conditions, i.e. non-photorespiratory conditions (BERRY & BJÖRKMAN, 1980), as found in this study (35-40ºC). According to Berry & Björkman (1980), this shift happens because there is CO_2 limitation for carboxylase reaction and/or changes in the ratio of photorespiratory CO_2 release to total photosynthetic CO_2 fixation under natural CO_2 concentration. Monson et al. (1982) found an increase around 10-15ºC in the optimum temperature for photosynthesis of a C3 species under low O_2 air concentration (2%) and high CO_2 concentration (800 μ mol mol^{-1}).

Both net and gross photosynthesis had the same pattern due to increasing temperature, but with significant differences when comparing the rates recorded at temperatures above 40ºC (Fig. 1A). In relation to this temperature threshold, gross and net photosynthesis were reduced in 6.8 and 16.9% at 45ºC, and 31.1 and 49.4% at 50ºC, respectively. Clearly, the gross photosynthesis was less affected because the respiratory activity was stimulated with increasing temperature (Fig. 1B). Accordingly, respiration is less sensitive than photosynthesis to heat stress, being abruptly inhibited at near-lethal temperature (HÄLLGREN et al., 1991). In fact, a temperature increase of 25ºC (from 25 to 50ºC) caused an increase of 4.8 times in leaf respiration under non-photorespiring conditions.

It is important to consider the beneficial interaction between the photosynthetic and respiratory processes, since mitochondrial metabolism is involved in the dissipation of excess redox equivalents (e.g. NADPH) from chloroplasts (RAGHAVENDRA & PADMASREE, 2003). Since an excess of reductants may be generated under stressful conditions such as high temperature, it is suggested that the increased respiratory activity observed at temperatures higher than 35ºC is an important protective mechanism of plant metabolism.

It is suggested that the heat stabilities of Rubisco and PEP carboxylase (Pepcase) are too high to account for all observed heat inhibition of photosynthesis in some species (BJÖRKMAN et al., 1980), being the decrease of photosynthetic activity caused by reductions of photochemical activity, thus whole-chain electron transport, generating an indirect thermal inactivation of other photosynthetic enzymes, such as NADP:glyceraldehyde-3P-dehydrogenase, ribulose-5P-kinase, and NADP:malate-dehydrogenase. The photochemical reactions are probably affected by damages on thylakoid membranes due to increase in the strength of hydrophobic bonds and decrease in the strength of hydrophilic bonds when increasing temperature (RAISON et al., 1980). In addition to the photochemical and consequent enzymatic impairments, high temperature also causes decreases of photosynthesis by reducing the leaf mesophyll conductance to CO_2 (KHAIRI & HALL, 1976). However, such an effect is probably negligible, since a saturating CO_2 concentration was applied in this study.

There was a stimulation of net and gross photosynthesis around 59.6 and 58.1%, respectively, when changing temperature from 25 to 40ºC, whereas the inhibition noticed from 40 to 50ºC was around 49.4 and 31.1% for net and gross photosynthesis respectively. It is important to note that the extension of heat damage depends on the exposure time (BERRY & BJÖRKMAN, 1980; GEORGIEVA, 1999) and light intensity (HÄLLGREN et al., 1991; KALITUHO et al., 2003; KOBZA & EDWARDS, 1987), being plants affected differently depending on species, variety and growth temperature (BERRY & BJÖRKMAN, 1980; RIBEIRO et al., 2004).

Since respiratory and photosynthetic processes are integrated and related (RAGHAVENDRA & PADMASREE, 2003), one could argue that a higher relationship between photosynthesis and respiration indicates that a higher amount of O_2 is released in relation to its consumption, which means high efficiency of atmospheric CO_2 gain. The highest A/R_d ratios were verified at 30 and 35ºC, being around 17 (Fig. 1D). This means that one O_2 molecule is released while 17 molecules of CO_2 are assimilated under non-photorespiratory condition. On the other hand, the lowest A/R_d ratio was found at 50ºC (Fig. 1D), indicating heat damage to plant metabolism. This stressful situation was not evident when comparing net photosynthetic rates at 25 and 50ºC, i.e. 15.3 and 18.7 μ mol m^{-2} s^{-1} respectively (Fig. 1A).

It is expected an optimized balance in the ratio of respiration to photosynthesis for maintaining and/or enhancing plant production or growth under varying environmental conditions (LAWLOR, 1995). So, it is reasonable to assume an optimum temperature in which the photosynthetic process takes place with high efficiency in relation to respiratory activity, being this temperature around 35ºC (Fig. 1D) under CO_2-saturating conditions. However, this optimum temperature should be lower under ambient CO_2 concentrations, as found in field conditions.

The light response curves of photosynthesis were affected by leaf temperature, being higher photosynthetic O_2 evolution observed at 40ºC (Fig. 2A). This higher photosynthetic activity was noticed at *PPFD* above 300 μ mol m^{-2} s^{-1}, showing an increasing trend until 1160 μ mol m^{-2} s^{-1}. These results indicate that the temperature treatment affected the photosynthetic capacity of leaf discs by increasing it at 40ºC, being probably caused by a shift of optimum temperature for photosynthesis under non-photorespiratory condition (BERRY & BJÖRKMAN, 1980). However, temperature treatment did not affect the overall quantum efficiency (Fig. 2A, Table 1).

The increase of temperature affected all photosynthetic parameters from light response curve (Table 1), with the exception of the overall quantum efficiency of photosynthesis. Monson et al. (1982) also found non-significant changes in the quantum efficiency of *Agropyrum smithii* Rydb. when varying leaf temperature from 20 to 35ºC under air CO_2 concentration of 800 μ mol mol^{-1} and 2% of O_2. Maximum photosynthetic rate increased by 68% as a result of shift in optimum temperature (Table 1), while dark respiration increased 3.7 times as a consequence of respiration stimulation caused by increased temperature (Table 1). Although the stimulation of dark respiration had increased the light compensation point, the observed values (Table 1) were lower than those ones measured under normal CO_2 atmospheric concentration (HABERMANN et al., 2003). This was probably caused by reduction of photorespiration under high CO_2 concentration, which permits a higher efficiency of Rubisco when considering the carboxylase activity in relation to the oxygenase one.

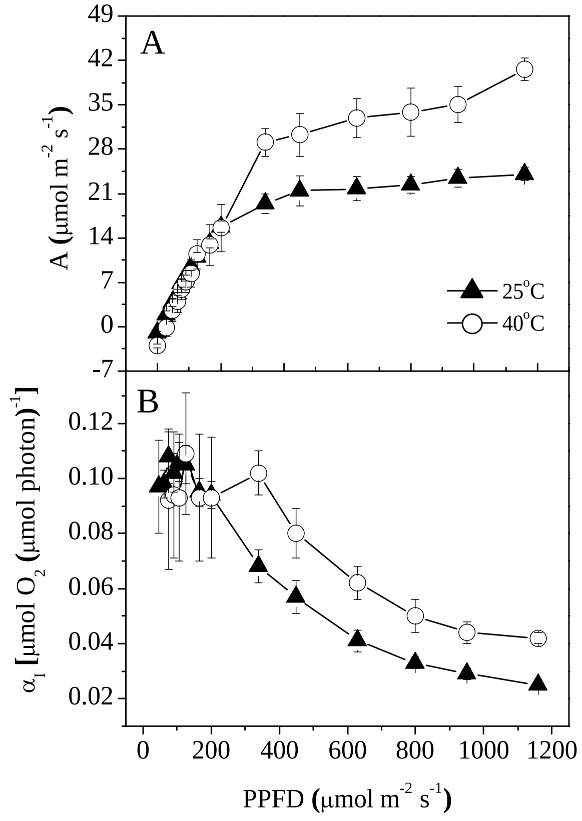

FIGURE 2 – Net photosynthesis (*A*, A) and instantaneous quantum efficiency of photosynthesis (α_I, B) a function of photosynthetic photon flux density (*PPFD*) in sweet orange leaf discs at 25ºC (closed triangles) and 45ºC (open circles) under non-photorespiratory condition. Each point represents the mean value (n=4) ± SE. Leaf discs were excised from plants grown under greenhouse conditions.

TABLE 1 – Photosynthetic parameters derived from light response curves in sweet orange leaf discs under non-photorespiratory condition at 25 or 40^{o}C: maximum photosynthetic rate (A_{max}), overall quantum efficiency of photosynthesis (α_O), dark respiration (R_d), light compensation ($PPFD_C$) and saturation ($PPFD_S$) points.

Photosynthetic parameters*	Leaf temperature (^{o}C)	
	25	40
A_{max} (μmol m^{-2} s^{-1})	24.06 ± 1.02	40.59 ± 1.73
α_O [μmol O_2 (μmol photon^{-1})]	0.114 ± 0.006	0.134 ± 0.018
R_d (μmol m^{-2} s^{-1})	0.96 ± 0.18	2.99 ± 0.29
$PPFD_C$ (μmol m^{-2} s^{-1})	7 ± 3	24 ± 6
$PPFD_S$ (μmol m^{-2} s^{-1})	628 ± 71	938 ± 133

* Mean values of three replications ± S.E.

As verified in this study (Table 1), light saturation of photosynthesis in citrus plants normally occurs between 600 and 1000 μmol m^{-2} s^{-1} (HABERMANN et al., 2003; MACHADO et al., 2005; RIBEIRO et al., 2003). However, the light saturation point was higher at 40^{o}C, indicating that more energy was necessary to allow the maximum photosynthetic activity. Regarding only the photosynthetic machinery, the biochemical enhancement caused by increased temperature probably determined or imposed a higher sink pressure on photochemical reactions that supply ATP and NADPH to CO_2 fixation. This assumption is in accordance to the higher instantaneous quantum efficiencies at 40^{o}C taken during the light response curve at *PPFD* higher than 300 μmol m^{-2} s^{-1} (Fig. 2B).

The decreasing trend of instantaneous quantum efficiency with increasing *PPFD* (Fig. 2B) is probably caused by closure of photosystem II (PSII) reaction center (MAXWELL & JOHNSON, 2000) due to increased energy availability for photochemistry (MEDINA et al., 2002). The effective quantum efficiency of PSII assessed by chlorophyll fluorescence is also reduced when increasing *PPFD* (RIBEIRO et al., 2003, 2005), revealing a regulatory mechanism to cope with light energy at PSII level. By reducing energetic pressure on reaction centers via decreased quantum efficiency, plants can potentially reduce the generation of oxygen reactive species and then avoid the deleterious effects of such molecules on photochemical reactions.

Under low *PPFD* (until 200 μmol m^{-2} s^{-1}), the instantaneous quantum efficiency is maximum and relatively stable, indicating that the electron transport rates at this *PPFD* range is sufficient to support the photosynthetic rates recorded (Fig. 2A). When increasing *PPFD*, the apparent electron transport rate is inversely proportional to the effective quantum efficiency of PSII (RIBEIRO et al., 2003). Considering this point, we can argue that the higher photosynthetic activity observed at 40^{o}C (Fig. 2A) was correlated with the higher photochemical activity (Fig. 2B), i.e. apparent electron transport rate, as verified in temperature response curve (Fig. 1A,C).

Some authors have reported that the early biochemical impairment caused by high temperature is caused by reduction of electron transport rates (BJÖRKMAN et al., 1980), however the results of this study (Fig. 1A,C and 2) do not suggest any photochemical injury due to high temperature when considered the range 25-50^{o}C and exposure time in each temperature (around 1.5 h in light response curves and 40 min. in temperature response curves). Regarding the photochemical impairment due to heat stress, the events leading to the loss of photosynthetic electron flow in potato leaves, a C3 species, under ambient CO_2 concentration are: inhibition of water splitting at temperatures higher than 32^{o}C; reduced energy trapping in PSII centers; changes in electron flow after the first stable electron acceptor from PSII, i.e. quinone (Q_A), at temperatures higher than 42^{o}C; impairment of PSI activity at temperatures higher than 45^{o}C (HAVAUX, 1993). However, it is important to consider that the differences in leaf anatomy among plant species, air CO_2 concentration, growth condition, and exposure time to high temperature are also important aspects related to heat sensitivity (BERRY & BJÖRKMAN, 1981; HÄLLGREN et al., 1991). Our results suggest that the electron transport inhibition by heat-damage begins at temperatures higher than 40 ^{o}C.

Although temperature response of photosynthesis may be influenced by several factors such as growth temperature, leaf age, light, water and nutrients (BERRY & BJÖRKMAN, 1980), it is expected a similar trend between leaves with approximate chlorophyll content, age, canopy position and growth conditions. As shown in Fig. 3, temperature responses of photosynthesis were different when comparing leaf tissues of plants growing in distinct conditions. Such a difference was more evident at temperatures higher than 40°C, the temperature threshold (Fig. 3). Considering that greenhouse showed a warmer internal environment than nursery condition, it is reasonable to assume that plants growing under greenhouse condition were acclimated to a warmer environment, being less sensitive to heat damage. In fact, the response of photosynthesis to temperatures higher than 40°C (Fig. 3) seems to support the above assumption related to plant acclimation, since plant tissues were fully expanded and exposed with similar age (around six months).

Regarding the measurements carried out at 45 and 50°C (Fig. 3), plants grown under warmer conditions showed a photosynthetic activity around 32% higher than those ones grown under nursery condition, revealing the acclimation of photosynthesis to high temperatures (BERRY & BJÖRKMAN, 1980). Some studies have reported increase in tolerance to heat stress in plants growing under warmer growth temperatures (GEORGIEVA, 1999). Accordingly, Havaux (1995) observed an adaptive mechanism in chloroplast processes that works as a sensing to moderate increase of environmental temperature, altering the PSII conformation to a more tolerant one in relation to heat stress. As citrus plants are evergreen species that are subjected to seasonal variation of temperature and other environmental factors (MACHADO et al., 2002), one can argue that such a species *a priori* has a greater acclimation potential of photosynthesis to high temperature (RIBEIRO et al., 2004). Björkman et al. (1980) concluded that plants differ greatly in their potential for photosynthetic acclimation to temperature, which is directly related to temperature regime of their native habitat.

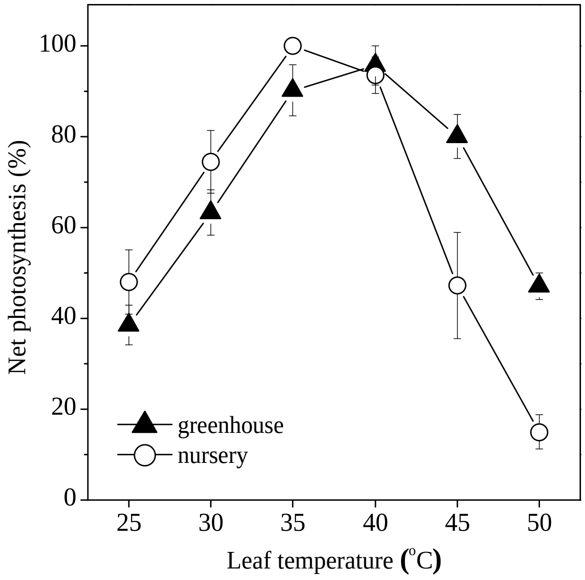

FIGURE 3 – Net photosynthesis as a function of leaf temperature in sweet orange leaf discs excised from plants grown under different conditions in relation to the environmental temperature: greenhouse and nursery conditions. Photosynthesis is expressed as % of maximum rates observed at 40°C (greenhouse) or 35°C (nursery). Each point represents the mean value (n=5) ± SE.

CONCLUSIONS

In sweet orange leaf discs under non-photorespiratory conditions:

- The optimum temperature range for photosynthesis is 35-40°C. However, the effects of heat damage to the plant metabolism are more evident when considering the balance between photosynthesis and respiration, which suggests an optimum temperature of 35°C;
- The stimulation of photosynthesis at 40°C increases the light saturation point without changing the quantum efficiency of photosynthesis under low light intensities. In addition, the enhancement of respiration by increasing temperature results in higher light compensation point;
- The heat stress sensitivity of photosynthesis is affected by growth temperature, indicating that sweet orange plants from warmer environments are more tolerant to heat stress.

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