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Comparison of thermotolerance of sun-exposed peel and shaded peel of 'Fuji' apple

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ABSTRACT

The thermotolerance of the sun-exposed peel and the shaded peel of 'Fuji' apple (*Malus domestica* Borkh.) fruit was evaluated by measuring pigments, chlorophyll *a* fluorescence transients and O_2 evolution or uptake after exposure to 25, 35, 40, 42, 44, 46 or 48 °C for 30 min in the dark. A major effect of heat stress at 46–48 °C on the chlorophyll *a* fluorescence transients was the appearance of a very clear K step at 200–300 μs for both peel types. The K step was slightly more pronounced in the sun-exposed peel than in the shaded peel, suggesting that the resistance of oxygen-evolving complex to heat stress is slightly lower in the sun-exposed peel than in the shaded peel. Minimal fluorescence (F_O), relative to the value at 25 °C, increased to a greater extent in the shaded peel than in the sun-exposed peel after exposure to 46–48 °C, but the temperature dependencies of F_O changes were similar for both peel types. Maximum quantum yield of PSII (F_V/F_M) decreased to a similar extent in the sun-exposed peel and the shaded peel as temperature rose from 25 to 44 °C, but the sun-exposed peel reached slightly lower values at 46–48 °C. Correspondingly, gross O_2 evolution rate, relative to that at 25 °C, was also slightly lower in the sun-exposed peel than in the shaded peel at 46–48 °C. In response to heat stress, the ratio of Q_A-reducing reaction centers (RCs) to total RCs and the ratio of Q_B-reducing RCs to Q_A-reducing RCs decreased, but both of them decreased to lower values in the sun-exposed peel than in the shaded peel at 46–48 °C, indicating that the capacity of electron transfer between P_{680}^+ and Q_B via Q_A was damaged to a greater extent in the sun-exposed peel than in the shaded peel. At each given temperature, dark respiration was similar between the two peel types. Overall, it appears that the exposure to higher surface temperature under high light does not make the sun-exposed peel more tolerant of heat stress than the shaded peel of apple fruit.

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1. Introduction

Fruit is more often exposed to heat stress than leaves as it has a higher surface temperature in the sun due to its very limited cooling capacity via transpiration (Cheng and Ma, 2004). Indeed, peel and flesh temperatures of the sun-exposed side of apple fruit can reach as high as 15 °C above ambient temperature even when the ambient temperature is below 30 °C (Ferguson et al., 1998). Similar results have been obtained in many other fruits (Brooks and Fisher, 1926; Millar, 1972; Woolf and Ferguson, 2000; Woolf et al., 2000). Once fruit peel temperature reaches a threshold, damage to the peel occurs. It has been reported that surface temperatures in the range between 45 and 49 °C lead to browning of the sun-exposed peel of apple fruit (sunburn browning), which significantly affects fruit finish and quality (Schrader et al., 2001). Our recent work showed that high temperature coupled with high light alters the balance between photooxidation and photoprotection in the sun-exposed peel of apple, and it appears that the damage to PSII is initiated by high temperature and exacerbated by high light (Chen et al., 2008). As global warming is expected to continue (Wigley, 2005), high temperature stress to fruit will become more of a problem, which points to the need to develop a better understanding of heat stress and the thermotolerance of fruit peel.

Photosynthesis is among the plant functions that are highly sensitive to heat stress, and it can be completely inhibited before other symptoms of heat stress are detected in leaves (Berry and Björkman, 1980). Heat stress can damage the oxygen-evolving complex (OEC) and the electron transport at both the donor and the acceptor sides of photosystems II (PSII) of the photosynthetic apparatus (Bukhov et al., 1990; Srivastava et al., 1997; Strasser, 1997; Kouřil et al., 2004; Sinsawat et al., 2004; Tóth et al., 2005; Lazár, 2006). Chlorophyll (Chl) *a* fluorescence transient has been used extensively to detect and understand heat stress-induced changes in the photosynthetic apparatus of leaves (Srivastava et al., 1997; Qiu and Lu, 2003; Wen et al., 2005; Jiang et al., 2006). For instance, a special "K" step often

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occurs during the Chl *a* fluorescence induction process due to the damage to OEC by heat stress (Guissé et al., 1995; Srivastava et al., 1997; Strasser, 1997; Hakala et al., 2005). This K step has been observed in the response of the sun-exposed peel to high temperature in the dark (Chen et al., 2008). However, the thermotolerance of apple peel has not been examined in detail using Chl *a* fluorescence transients.

Since fruit has both a sun-exposed side and a shade side, comparison of the sun-exposed side with the shaded side may provide insights into the mechanism by which they respond and adapt to light and temperature stresses. Our previous work showed that the sun-exposed side of apple fruit has higher photosynthetic capacity and higher xanthophyll cycle pool size and antioxidants (Ma and Cheng, 2003; Chen and Cheng, 2007; Li and Cheng, 2008). However, it is not known whether the sun-exposed peel of apple also has a higher tolerance to heat stress than the shaded peel. Woolf et al. (2000) reported that the sun-exposed side of avocado (*Persea americana* Mill.) fruit sustained less damage than the shaded side in response to high temperature treatments (50 °C for 7.5 min or 55 °C for 7.5 min) in water. Considering the sun-exposed peel experiences higher surface temperature than the shaded peel on a regular basis, we reasoned that this would increase the thermotolerance of the sun-exposed peel of apples as that observed in avocado. In this study, we investigated the changes of Chl *a* fluorescence transient, photosynthetic O_2 evolution, respiration, and pigments in response to heat stress to determine whether the sun-exposed peel has higher thermotolerance than the shaded peel of apple fruit.

2. Materials and methods

2.1. Plant materials

Seven-year-old 'Fuji' apple (*Malus domestica* Borkh.) trees on M.9 rootstocks were grown at a spacing of 2.4 m × 4.2 m in the field at a Cornell research farm in Lansing, New York, USA. The trees were trained in a spindle system. They were approximately 3.0 m tall. They received standard horticultural practices, diseases and pest control. On 19–22 August 2006, approximately 100 days after full bloom, sun-exposed fruit was chosen from the west side of the canopy for temperature treatments. Fruit fresh weight, diameter and length are 61.4 ± 1.89 g FW fruit^{-1}, 51.8 ± 0.6 mm and 42.6 ± 0.5 mm, respectively.

2.2. Temperature treatments

Fruit was taken right after sunset and wrapped in wet paper towel. After overnight dark adaptation, peel discs (ca. 1 cm^2 in size and 1 mm thick) were cut from both the sun-exposed side and the shaded side of the fruit. They were wrapped in wet paper towel and placed onto the smooth bottom of a small vessel (1.5 cm in height × 6.2 cm in diameter) made of aluminum foil. Then, the vessel was directly floated on water. Water temperature was controlled by a refrigerated water bath (NESLAB RTE-10, Thermo Electron Corp., NH, USA). Temperature equilibrium between peel discs and water was reached within 3 min. The peel discs were exposed to different temperatures (25–48 °C) in the dark for 30 min. Chl *a* fluorescence transient, pigment content, dark respiration and photosynthetic O_2 evolution capacity were measured after heated peel had been kept in the dark for 30 min at room temperature. All measurements were performed at room temperature. In our preliminary experiments, detached fruit wrapped in wet paper towel and peel discs (1 cm^2 each, 1 mm thick) kept on wet cheese cloth were found to maintain their photosynthesis and Chl fluorescence properties unchanged for at least 48 and 4 h, respectively.

2.3. Measurements of dark respiration and photosynthetic O_2 evolution rates

Dark respiration and photosynthetic O_2 evolution rates of peel discs were measured with a ChloroLab-2 liquid-phase oxygen electrode system (Hansatech Instruments, Norfolk, UK) as described previously (Chen and Cheng, 2007). Briefly, after the heat-treated peel discs were kept in the dark for 30 min, they were cut into smaller peel discs (0.4 cm^2 in size, 0.5 mm thick) with a cork-borer and a sharp razor. Each peel disc was immediately placed into the reaction chamber filled with 1.5 ml 50 mM Hepes-KOH, pH 7.2, 0.5 mM $CaSO_4$ and 20 mM $NaHCO_3$ (Yoshida et al., 2006). After 5 min equilibration in darkness, dark respiration was measured and the data were continuously monitored for 10 min. Then, the peel disc was exposed to 500 μmol m^{-2} s^{-1} PFD, which was provided by an array of light-emitting diodes (LEDs peak emission at 650 nm). After 10 min equilibration under light, O_2 evolution was measured and the data were continuously monitored for 10 min. Net O_2 exchange rate was calculated over the last 3 min.

2.4. Measurements of Chl a fluorescence transient

Polyphasic Chl *a* fluorescence transient was measured with a Handy PEA (Hansatech Instruments, Norfolk, UK) after the temperature-treated peel was dark-adapted for 30 min. The transient was induced by red light of 3000 μmol photons m^{-2} s^{-1} provided by an array of three light-emitting diodes (peak 650 nm) for 5 s, which was focused on the fruit peel surface to give homogenous illumination over the exposed area of the fruit peel (4 mm in diameter). Initially, data were sampled at 10 μs intervals for the first 300 μs, then, the time resolution of digitisation was switched to slower acquisition rates.

Chl *a* fluorescence transient was analyzed by using JIP-test (Strasser et al., 2000, 2004; Appenroth et al., 2001; Force et al., 2003). Maximum quantum yield of PSII (F_V/F_M) was calculated as $F_V/F_M = (F_M - F_O)/F_M$. Relative variable fluorescence intensity at K step (V_K), J step (V_J) and I step (V_I) were calculated as $V_t = (F_t - F_O)/(F_M - F_O)$, where $F_t = F_K$, F_J, and F_I. Ratio of variable fluorescence at K step to the amplitude $F_J - F_O$ (W_t) was calculated as $W_t = (F_t - F_O)/(F_J - F_O)$.

Ratio of Q_A-reducing PSII reaction centers (RCs) to total PSII RCs (RC_{Q_A}) was calculated as $RC_{Q_A} = (RC/CS_X)/(RC/CS_{ck})$, where RC/CS was the density of Q_A-reducing PSII RC per excited cross-section (RC/CS; CS, excited cross section), calculated as $RC/CS = F_V/F_M \times (V_J/M_O) \times (ABS/CS)$, $M_O = 4 \times V_K$, $ABS/CS \approx F_O$ (Strasser et al., 2000, 2004; Force et al., 2003). In this study, all the PSII RCs in the shaded peel at 25 °C (RC/CS_{ck}) were assumed as Q_A-reducing PSII RCs and were taken as control, namely in the shaded peel before heat stress treatment, $RC_{Q_A} = 1$.

Ratio of Q_B-reducing RCs to Q_A-reducing RCs (RC_{Q_B}) was estimated following the protocol for so-called double hit experiments as described by Appenroth et al. (2001). Dark-adapted peel discs were exposed to a saturating light (3000 μmol photons m^{-2} s^{-1}) for 5 s twice with a 10 s interval in the dark. RC_{Q_B} was calculated as $(F_V/F_M)^2/(F_V/F_M)^1$, where $(F_V/F_M)^1$ was the F_V/F_M value after the peel was exposed to the saturating light for the first time, and $(F_V/F_M)^2$ was the value of F_V/F_M after the peel was exposed to the saturating light twice.

2.5. Analysis of peel pigments

Chls and carotenoids were assayed according to Lichtenthaler (1987). Briefly, 4 discs of apple peel (ca. 1 cm^2 in size and 1 mm thick) were extracted with 3 ml of 80% (v/v) acetone for 24 h in

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