Ultraviolet radiation effects on fruit surface respiration and chlorophyll fluorescence

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SUMMARY
High-value fruit crops are exposed to a range of environmental conditions that can reduce fruit quality. Solar injury (SI) or sunburn is a common disorder in tropical, sub-tropical, and temperate climates and is related to: 1) high fruit surface temperature; 2) high visible light intensity; and, 3) ultraviolet radiation (UV). Positional changes in fruit that are caused by increased weight or abrupt changes that result from Summer pruning, limb breakage, or other damage to the canopy can expose fruit to high solar radiation levels, increased fruit surface temperatures, and increased UV exposure that are higher than the conditions to which they are adapted. In our studies, we examined the effects of high fruit surface temperature, saturating photosynthetically-active radiation (PAR), and short-term UV exposure on chlorophyll fluorescence, respiration, and photosynthesis of fruit peel tissues from tropical and temperate fruit in a simulation of these acute environmental changes. All tropical fruits (citrus, macadamia, avocado, pineapple, and custard apple) and the apple cultivars ‘Gala’, ‘Gold Rush’, and ‘Granny Smith’ increased dark respiration (A0) when exposed to UV, suggesting that UV repair mechanisms were induced. The maximum quantum efficiency of photosystem II (Fv/Fm) and the quantum efficiency of photosystem I (ΦI) were unaffected, indicating no adverse effects on photosystem II (PSII). In contrast, ‘Braeburn’ apple had a reduced Fv/Fm with no increase in A0 on all sampling dates. There was a consistent pattern in all studies. When Fv/Fm was unaffected by UV treatment, A0 increased significantly. Conversely, when Fv/Fm was reduced by UV treatment, then A0 was unaffected. The pattern suggests that when UV repair mechanisms are effective, PSII is adequately protected, and that this protection occurs at the cost of higher respiration. However, when the UV repair mechanisms are ineffective, not only is PSII damaged, but there is additional short-term damage to the repair mechanisms, indicated by a lack of respiration to provide energy.

High-value fruit crops are exposed to a range of environmental conditions that can reduce fruit quality, while markets demand an almost perfect fruit appearance. Solar injury (SI) or sunburn is a common disorder in tropical, sub-tropical, and temperate climates. There are three general environmental factors related to SI: 1) high fruit surface temperature; 2) high visible light intensity; and, 3) ultraviolet radiation (UV; UV-A 320-400 nm; UV-B 280-320 nm; Woolf and Ferguson, 2000; Wünsche et al., 2001; Schrader et al., 2001). Fruits of different species respond differently to these three environmental factors (reviewed in Glenn et al., 2002). Tropical regions experience higher levels of UV radiation than do temperate zones at higher latitudes, because of the small solar zenith angle and the thinner stratospheric ozone layer (Krause et al., 1999; Madronich et al., 1998) and, depending upon the season, can have long periods of high temperatures and clear skies that result in SI damage. UV-B radiation damages PS II, and the effects can be measured through a reduction in variable chlorophyll fluorescence (Jansen et al., 1998), UV-A radiation causes increased formation of reactive molecules and decreased electron transport efficiency (White and Jahnke, 2002).

Plant mechanisms to protect tissues from SI damage are based primarily on secondary pigment development (Demmig-Adams and Adams, 1992), including increased synthesis of flavonoids (Solovchenko and Schmitz-Eiberger, 2003) and carotenoids. However, anthocyanins are not effective secondary pigment protectants at low and moderate levels (Solovchenko and Schmitz-Eiberger, 2003; Woodall and Steward, 1998). Early degradation of chlorophyll and reduced chlorophyll fluorescence are indicators of SI damage in fruit (Wünsche et al., 2001). Because mature and chlorophyll-free peppers and cucumbers did not respond by developing SI damage under high UV light, Rabinowitch et al. (1983; 1986) reasoned that chlorophyll, and its
subsequent degradation, was also a causal agent of SI. Fruit, unlike leaves, generally lose chlorophyll during the maturation process, concomitant with an increase in the concentration of anthocyanins and carotenoids (Reay and Lancaster, 2001; Reay et al., 1998). However, Cheng (L. Cheng, personal communication) noted decreased carotenoid and xanthophyll cycle pigment levels as apple fruit developed. The development of anthocyanins (Chalmers and Faragher, 1977a,b) and carotenoids (Solvokhenko and Schmitz-Eiberger, 2003), xanthophyll cycle pigments (Krause et al., 1999), and flavonoids (Reay and Lancaster, 2001) increased with increasing photosynthetically-active radiation (PAR) and UV radiation. In contrast, high temperatures reduced their development (Saure, 1990).

Positional changes in fruit caused by increased weight or abrupt changes due to Summer pruning, limb breakage, defoliation by insects, or other damage can expose fruit to higher levels of solar radiation, increased fruit surface temperatures, and increased UV exposure, higher than those to which they are adapted. These acute changes in environmental conditions can result in SI damage in all climates. To understand the effect of environmental factors on SI, we examined the short-term effect of a high fruit surface temperature (40°C), saturating PAR (1,000 µmol m–2 s–1), and short-term UV-A (19.5 W m–2; from 320 – 400 nm) exposure on chlorophyll fluorescence, respiration, and photosynthesis in fruit peel tissues of tropical and temperate fruits, in a simulation of these acute environmental changes.

MATERIALS AND METHODS

Tropical fruit studies.

The species sampled were: 1) citrus [Citrus sinensis (L.) Osb., cv. Valencia]; 2) macadamia (Macadamia integrifolia Maiden and Betch, cv. 847); 3) avocado (Persea americana Mill., cv. Hass); 4) pineapple (Ananas comosus Merr., cv. Smooth Cayenne); and 5) custard comosus (Maiden and Betche, cv. 847); 3) avocado (L.) Osb., cv. Valencia]; 2) macadamia (Macadamia because of canopy coverage. A 1 cm2 core of fruit peel were oriented toward the sun, but not fully exposed a.s.l.).

Nambour, Queensland, Australia (26.4ºS; 152.6ºE; 31 m a.s.l.). Baseline data were collected on 26 and 27 March 2004 at the Maroochy Research Station, Nambour, Queensland, Australia (26.4ºS; 152.6ºE; 31 m a.s.l.).

Peel samples were collected from fruit tissues that were oriented toward the sun, but not fully exposed because of canopy coverage. A 1 cm2 core of fruit peel and flesh was extracted from each fruit. The length of the core was cut to 3 – 5 mm. The core was placed on a glass slide, and the base and exposed edges were coated with silicone grease to prevent gas exchange from surfaces other than the peel. The peel core was then placed inside the cuvette of a photosynthesis system (CIRAS-2; PP Systems, Amesbury, MA, USA). The cuvette CO2 concentration was 500 µl l–1. The cuvette had two ports oriented to the centre of the cuvette: 1) an entry for the chlorophyll fluorescence probe (FMS2 Hansatech; PP Systems); and, 2) an entry for a fibre optic probe from a PAR source (Model LC5; Hamamatsu Inc., Middlesex, NJ, USA). Two optical filters were installed in the path of the radiation from the UV source: 1) a Hoya U-340 25 mm square (NT46-084; Edmund Optics Inc., Barrington, NJ, USA), which had a peak transmission at 340 nm and excluded visible and infrared wavelengths; and, 2) a UV transmission filter that passed approx. 85% of radiation less than 400 nm, but blocked 400 – 700 nm (A7028-03; Hamamatsu Inc.). The UV source provided 19.5 W m–2 from 320 – 400 nm, or about 50 – 60% of the natural incoming UV-A intensity at solar noon (30 – 40 W m–2; Krause et al., 1999). The UV source had a UV-A:UV-B ratio of 26:1, while natural sunlight is approx. 20:1 (Krause et al., 1999). Radiation intensity from 200 – 290 nm was 0.5 W m–2. The cuvette temperature was 40°C, PAR was either 0 or 1,000 µmol m–2 s–1; and the UV source was alternately “off” and “on” at both PAR levels. Peel samples were placed in the centre of the cuvette and brought to 40°C in the dark, without UV, for 10 min equilibration. Following temperature and light equilibration, gas exchange and chlorophyll fluorescence were measured every 7 min. At PAR = 0, net photosynthesis (A0) was measured and interpreted as dark respiration, and the maximum quantum efficiency of photosystem II (Fv/Fm) was measured.

The treatment sequence was: 1) PAR = 0, UV = off; 2) PAR = 0, UV = on; 3) PAR = 0, UV = off; 4) PAR = 0, UV = on. PAR was then set at 1,000 µmol m–2 s–1 for 10 min at 40°C. At PAR = 1,000, net photosynthesis (A1,000) was measured and the quantum efficiency of photosystem II (ΦII) was measured under saturating light conditions.

The next treatment sequence was: 1) PAR = 1,000, UV = off; 2) PAR = 1,000, UV = on; 3) PAR = 1,000, UV = off; and 4) PAR = 1,000, UV = on. Six replicates of each fruit were measured. Data were statistically analysed by species and by PAR level to test the effect of UV treatment at each PAR level, pooled over the alternate UVoff and UVon conditions. The difference in response (UVon minus UVoff) for A0, A1,000, Fv/Fm, and ΦII (respectively indicated as ∆A0, ∆A1,000, ∆Fv/Fm, and ∆ΦII) was tested against a value of 0 with a t-test (P = 0.05) at each PAR level.

Apple studies

Study 1: ‘Braeburn’ apple [Malus sylvestris (L.) Mill. var. domestica (Borkh.) Mansf.] on M.9 rootstock was grown in a 30 l container for 3 years at Palmerston North, New Zealand (40.4ºS; 175.6ºE; 45 m a.s.l.). After petal fall in 2003, eight plants were placed beneath a polycarbonate structure that excluded 98% of UV radiation, but blocked 400 – 700 nm, and retained 40 – 50% of the natural sunlight. At PAR = 0, net photosynthesis (A0) was measured and interpreted as dark respiration, and the maximum quantum efficiency of photosystem II (ΦII) was measured under saturating light conditions.

The next treatment sequence was: 1) PAR = 1,000, UV = off; 2) PAR = 1,000, UV = on; 3) PAR = 1,000, UV = off; and 4) PAR = 1,000, UV = on. Six replicates of each fruit were measured. Data were statistically analysed by species and by PAR level to test the effect of UV treatment at each PAR level, pooled over the alternate UVoff and UVon conditions. The difference in response (UVon minus UVoff) for A0, A1,000, Fv/Fm, and ΦII (respectively indicated as ∆A0, ∆A1,000, ∆Fv/Fm, and ∆ΦII) was tested against a value of 0 with a t-test (P = 0.05) at each PAR level.

Eight plants were maintained nearby under ambient conditions (i.e., without a UV filter). Within the UV filter treatments, four trees were treated with a 3% reflective kaolin spray (PF) every 2 weeks (Surround WP Crop Protectant; Engelhard Corp., Iselin, NJ, USA). There were approx. 40 fruit on each tree. Thirty days before maturity, two trees of each treatment were selected and the fruit used in subsequent studies. Trees were selected based on uniformity of cropping and vegetative growth.

Baseline data were collected on 26 and 27 March 2004. Peel samples from the exposed shoulders of fruit were measured, as in the tropical fruit studies, for A0, A1,000, Fv/Fm, and ΦII. The residue from the PF treatment was
removed before measurement. In addition, the chlorophyll $a$ and $b$ (Chl), anthocyanin, and carotenoid concentrations of fruit, at the site of sampling, were estimated from reflectance measurements, according to Merzlyak et al. (2003). Reflectance was measured with a spectral radiometer (Model EPP 2000; StellarNet Inc.). Data for $A_0$, $A_{1,000}$, $Fv/Fm$, and $\Phi II$ were analysed in a split-plot design with the UV filter as the main plot, and PF treatment as the sub-plot, with six replicates of individual fruit, pooled over alternating UV$_{off}$ and UV$_{on}$ cycles at each PAR level. The difference in response (UV$_{off}$ minus UV$_{on}$) for $\Delta A_0$, $\Delta A_{1,000}$, $\Delta Fv/Fm$, and $\Delta \Phi II$ was tested against a value of 0 with a $t$-test ($P = 0.05$) at each UV filter and PF treatment level, for each PAR level.

Four trees, one representing each treatment, were placed in growth chambers under either 24ºC day/19ºC night, or 40ºC day/19ºC night conditions (New Zealand Controlled Environmental Laboratory, Palmerston North, New Zealand). The vapour pressure deficit was 1.0 kPa for all temperatures, the CO$_2$ concentration was 500 µl l$^{-1}$, and PAR was 1,350 µmol m$^{-2}$ s$^{-1}$ with a 10 h photoperiod. Illumination provided 12 W m$^{-2}$ of UV from 300 – 400 nm.

Fruits were collected from the trees in the growth chambers after 5 d and 10 d and measured in a manner similar to that used in the baseline studies.

Data for $A_0$, $A_{1,000}$, $Fv/Fm$, and $\Phi II$ were analysed in a split-plot design with four individual fruit replications. The main plot was the growth chamber day temperature, the sub-plot was the UV filter, and the split-split plot was the PF treatment, pooled over the alternate UV$_{off}$ and UV$_{on}$ cycles at each PAR level. The difference in response (UV$_{off}$ minus UV$_{on}$) for $\Delta A_0$, $\Delta A_{1,000}$, $\Delta Fv/Fm$, and $\Delta \Phi II$ was tested against a value of 0 with a $t$-test ($P = 0.05$) at each chamber temperature, UV filter, and PF treatment level, for each PAR level. Mean separation used a protected Duncan’s multiple range test ($P = 0.05$) at each sampling date.

Study 2: ‘Gala’ apple on M.9 rootstock were planted in 1999 at 1 m × 6 m spacing in a North-South orientation at the USDA-ARS-Appalachian Fruit Research Station, Kearneysville, WV (39.4 N; 77.9 W; 169 m a.s.l.). In 2004, UV filters made from polycarbonate frames (5.0 m × 2.4 m × 0.8 mm) were constructed and placed at 60º and 120º angles adjacent to the trees. This arrangement of two panels on either side of the trees resulted in a pyramidal-shaped enclosure with a 0.5 m opening at the top and a 2.0 m opening at the bottom. Five trees were contained within each enclosure. The end of the frame within the tree row was left open. The panels were left on the trees from petal fall until harvest, and removed for a 24 hr period every 2 weeks for pest control application. The experimental design consisted of three treatments: 1) untreated control; 2) enclosure in the UV filter frames; and, 3) application of 3% kaolin spray (PF) every 2 weeks from petal fall until harvest, in a randomised complete block design with four replications of four trees per plot. Trees were hand-thinned to approx. 100 fruit per tree. Two representative fruit from each plot were collected on 21 June, 27 July, and 26 August 2004 from the three central trees per plot. Fruit peel samples from the exposed side of each fruit were measured for $A_0$, $A_{1,000}$, $Fv/Fm$, $\Phi II$, and pigments (Chl, anthocyanins, and carotenoids) by reflection, as described above. After the data from the peel samples had been collected, the attached pulp was removed and the peel was frozen in liquid nitrogen. Chlorophyll $a$ and $b$ and xanthophyll pigments (violaxanthin, antheraxanthin, and zeaxanthin; VAX) from two fruit peel discs (total area, 2 cm²) per plot were measured by a procedure described in Cheng (2003).

Data for $A_0$, $A_{1,000}$, $Fv/Fm$, and $\Phi II$ were analysed in a randomised complete block design with three blocks in which two fruit were sampled from each plot, and the data pooled over the alternation of UV$_{off}$ and UV$_{on}$ cycles at each PAR level. The difference in response (UV$_{off}$ minus UV$_{on}$) for $\Delta A_0$, $\Delta A_{1,000}$, $\Delta Fv/Fm$, and $\Delta \Phi II$ was tested against a value of 0 with a $t$-test ($P = 0.05$) at each treatment level, at each PAR level. Pigment concentration was analysed in a randomised complete block design with three blocks, pooling data from the two fruit samples. Mean separation used a protected Duncan’s multiple range test ($P = 0.05$) at each sampling date.

In 2004, air temperature, PAR, and UV radiation within the enclosures, and in adjacent untreated trees, were measured from 3 – 5 September. Five thermocouples were installed within a single enclosure: two at 0.5 m and two at 3 m height, with one thermocouple on the East side of the canopy, and one on the West side of the canopy. Thermocouples were located at a depth of 20 – 30 cm within the enclosure. Air temperature above the enclosure was measured at 3.5 m above ground-level with a shaded thermocouple. A similar pattern of instrumentation was established in an adjacent, untreated plot without the enclosure. Data were collected every 5 s, and an hourly average computed. PAR and UV radiation were measured in each plot with two spectral radiometers (Model EPP 2000; StellarNet Inc.) on 3 – 5 September. Data were measured every hour. The two radiation sensors were calibrated against a known source. The sensor was positioned between two trees at a height of 1 m in each plot area.

Study 3: ‘Granny Smith’ and ‘Gold Rush’ apples planted in 1998 on M.26 rootstock at a 2 m × 5 m spacing at the USDA-ARS-AFRS were sampled on 27 November 2004. Fruit peel samples from the exposed side of each fruit were measured for $A_0$, $A_{1,000}$, $Fv/Fm$, and $\Phi II$, as described. Four replicates of each fruit were measured. Data were analysed by PAR level to test the effect of UV treatment at each PAR level, pooled over the alternating UV$_{off}$ and UV$_{on}$ cycles. The difference in response (UV$_{off}$ minus UV$_{on}$) for $\Delta A_0$, $\Delta A_{1,000}$, $\Delta Fv/Fm$, and $\Delta \Phi II$ was tested against a value of 0 with a $t$-test ($P = 0.05$) at each PAR level.

RESULTS

In apple Study 2 with ‘Gala’, the polycarbonate transmitted 95% of PAR and excluded 97% of UV radiation under the test conditions; however, in the field, 100% of PAR was measured within the enclosure, and UV was reduced by 75% daily (Figure 1). Midday temperatures were increased by 3º – 4ºC at 2 m height on sunny days, and less than 1ºC on cloudy days (Figure 2). At 0.5 m height, air temperature was increased 1º – 3ºC at
UV effects on fruit surface physiology

midday on sunny days, and approx. 1°C on a cloudy day. The UV treatment increased respiration (Figure 3), resulting in a more negative value when comparing CO₂ assimilation with UV off minus UV on. Leaf temperature increased by 0.1°C when the UV lamp was used. The response of fruit peel to UV radiation was reversible. This example illustrates a minimal, but significant, response (ΔA₀ = 0.2) in apple.

In all studies A₁₀₀₀, ΔΦII, ΔA₁₀₀₀, and ΔΦII were unaffected by the treatments (data not shown; P = 0.05).

Chlorophyll a and b concentrations, measured by reflectance, correlated with chemical analysis (y = 0.87x – 2.08; r² = 0.85, P = 0.05). Anthocyanin and carotenoid concentrations measured by reflectance were not chemically validated.

**Tropical fruit study**

At PAR = 0, the presence of UV radiation increased the production of CO₂ in all species (Table I). The increased production of CO₂ (more negative value) was interpreted as increased dark respiration (A₀). ΔFv/Fm was unaffected by the presence of UV radiation.
Pineapple, a crassulacean acid metabolism (CAM) plant, exhibited C₃ assimilation in the peel.

**Apple studies**

**Study 1:** A₀, A₀/ΦII, Fv/Fm, and pigments data collected after 0, 5 and 10 d in the growth chamber, indicated no effect (P = 0.05) of the particle film (PF) treatments; therefore, data were pooled over the PF treatments at all sampling dates.

At 0 d in the growth chambers, peel Fv/Fm was unaffected by the UV filter, but the peel response beneath the UV filter showed a greater depression in ΔFv/Fm than the control (Table II). Fruit grown beneath the UV filter had chlorophyll levels equivalent to those of the ambient, but reduced carotenoids and anthocyanins (Table II). There were no significant interactions.

After 5 d in the growth chambers, peel grown beneath the UV filter had the lowest Fv/Fm and the greatest ΔFv/Fm (Table II) compared to the control treatments at both 28ºC and 40ºC. There was an interaction of growth chamber temperature with the UV filter treatment after 5 d in the growth chamber, in which peel grown beneath the UV filter had reduced carotenoid and anthocyanin levels (Table II) compared to ambient UV; and 40ºC day temperature further reduced the levels of anthocyanins (Table II). There were no significant interactions.

After 10 d in the growth chambers, Fv/Fm was lower and ΔFv/Fm was greater for fruit grown beneath the UV filters. Carotenoids and anthocyanin levels were decreased in apple peel by the UV filter and 40ºC growth chamber temperature (Table II). There were no significant interactions.

**Study 2:** On the 21 June 2004 sampling, peel samples from fruit grown beneath the UV filter had a greater ΔFv/Fm with reduced anthocyanins and carotenoids, compared to the control and PF treatments (Table III). ΔA₀ was significantly greater than 0, but there were no treatment effects. On the 27 July 2004 sampling, chlorophyll fluorescence and A₀ were unaffected by all the treatments. Anthocyanins and carotenoids were lowest for the UV filter treatment, and highest for the control, with the PF treatment being intermediate. ΔA₀ was significantly greater than 0, but there were no treatment effects. On the 26 August sampling, the PF treatment had the highest Fv/Fm response, but there were no differences in ΔFv/Fm response to UV treatment. Anthocyanins were highest in the control and PF treatments, and lowest in the UV filter treatment. Carotenoids were highest in the control, lowest in the UV filter, and the PF treatment was intermediate. ΔA₀ was not significantly greater than 0 at this sampling time. Chlorophyll a and b and the xanthophyll pool declined over the three sampling dates, but did not demonstrate any treatment effect at any date, whereas carotenoid and anthocyanin levels increased over the three sampling dates. On all three sampling dates, there was no significant treatment effect on the xanthophyll (VAZ) pool; however, the trend was for the control and PF treatments to have higher xanthophyll contents than the UV filter treatment.

**DISCUSSION**

The response of fruit peel A₀ to UV radiation was rapid (Figure 3) and was demonstrated in both tropical (Table I) and temperate fruits (Tables II–IV). UV radiation, and UV-B in particular, damages DNA (Britt, 1996) and the photosynthetic apparatus (Jansen et al., 1998). The response of fruit peel to UV radiation was different.

### Table I

<table>
<thead>
<tr>
<th>Fruit Crop (cultivar)</th>
<th>Fv/Fm (ΔFv/Fm)</th>
<th>A₀ (ΔA₀) (µmol m⁻² s⁻¹)</th>
<th>Chlorophyll a + b (mmol m⁻²)</th>
<th>Carotenoids (mmol m⁻²)</th>
<th>Anthocyanins (mmol m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pineapple ('Smooth cayenne')</td>
<td>0.71 (0.0)</td>
<td>-5.1 (0.9)*</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
<tr>
<td>Custard apple ('African pride')</td>
<td>0.67 (0.0)</td>
<td>-6.8 (0.6)*</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
<tr>
<td>Avocado ('Hass')</td>
<td>0.76 (0.0)</td>
<td>-5.4 (1.9)*</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
<tr>
<td>Citrus ('Valencia')</td>
<td>0.45 (0.01)</td>
<td>-6.6 (0.5)*</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
<tr>
<td>Citrus ('suma')</td>
<td>0.45 (0.01)</td>
<td>-6.6 (0.5)*</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
</tbody>
</table>

### Table II

<table>
<thead>
<tr>
<th>Growth Conditions</th>
<th>Chamber Temperature</th>
<th>UV Filter</th>
<th>Fv/Fm (ΔFv/Fm)</th>
<th>A₀ (ΔA₀) (µmol m⁻² s⁻¹)</th>
<th>Chlorophyll a + b (mmol m⁻²)</th>
<th>Carotenoids (mmol m⁻²)</th>
<th>Anthocyanins (mmol m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient</td>
<td>Ambient</td>
<td>(-)</td>
<td>0.69 (0.04)*</td>
<td>-3.0 (0.0)</td>
<td>30</td>
<td>341 a</td>
<td>163 a</td>
</tr>
<tr>
<td>5 d in growth chamber</td>
<td>28ºC</td>
<td>(-)</td>
<td>0.70 a (0.05)* b</td>
<td>-1.4 (-0.1)</td>
<td>26</td>
<td>253 a</td>
<td>139 a</td>
</tr>
<tr>
<td>10 d in growth chamber</td>
<td>28ºC</td>
<td>(+)</td>
<td>0.61 b (0.10)* a</td>
<td>-1.7 (-0.0)</td>
<td>23</td>
<td>189 b</td>
<td>94 b</td>
</tr>
<tr>
<td>Pooled</td>
<td>Pooled</td>
<td>(-)</td>
<td>0.67 a (0.04)* b</td>
<td>-1.7 (0.0)</td>
<td>19</td>
<td>255 a</td>
<td>116 a</td>
</tr>
<tr>
<td>20ºC</td>
<td>28ºC</td>
<td>(-)</td>
<td>0.70 a (0.04)* b</td>
<td>-1.3 (0.0)</td>
<td>21</td>
<td>64 c</td>
<td>48 c</td>
</tr>
</tbody>
</table>

**NS, no significant difference (P = 0.05).**

*Significant difference (P = 0.05) based on a t-test (UVa₀ minus UVa₀) = 0.

*Values followed by different lower-case letters indicate a significant difference (P = 0.05) based on a protected Duncan’s Multiple Range test by sample date.

Growth chambers were maintained at 28ºC or 40ºC. Data were collected after 0, 5, and 10 d. The peel received 7 min exposure to 20 W m⁻² UV radiation (Apple Study 1).

Values in parentheses are the response (ΔFv/Fm and ΔA₀) at UVa₀ minus UVa₀.
similar to the tissue responses of other species. Krause et al. (1999) demonstrated a decline in $F_v/F_m$ in Virola surinamensis (Rol.) Warb. leaves within 10 min of UV treatment at approx. 42 W m$^{-2}$. Some algal species demonstrate reversible and increased $A_o$ with 2 W m$^{-2}$ UV-B (Beardall et al., 1997); and 0.2 W m$^{-2}$ UV-A inhibited alternative respiration, but stimulated CN-sensitive respiration (Mulley et al., 2001) with 1 – 6 h exposures. Increased dark respiration has been associated with moderate levels of UV radiation (Gwynn-Jones, 2001; Brandle et al., 1977; Sisson and Caldwell, 1976; Ziska et al., 1991) and was attributed to increased resource demands for protection and repair (Gwynn-Jones, 2001). All tropical fruit increased $A_o$ when challenged with UV, suggesting that UV repair mechanisms are induced and functioning with no adverse effect on photosystem II, since $F_v/F_m$ and $\Phi II$ were unaffected. Tropical plants have evolved and have been domesticated under higher UV levels and, based on our findings, robust UV protection mechanisms are active in a range of tropical species. Krause et al. (1999) demonstrated that leaves of tropical plants can become fully protected against UV radiation, depending on their light acclimation and developmental stage. Tolerance of tropical species to UV was attributed to UV-absorbing substances, including anthocyanins, carotenoids, and VAZ, that increase with exposure in fully-illuminated leaves. Similarly, the photosynthetic rate of soybean leaves adapted to UV-B was unaffected by a UV-B challenge of approx. 0.5 W m$^{-2}$; however, the photosynthetic rate of non-adapted leaves was reduced by 20% (Mirecki and Teramura, 1984). UV radiation, in general, and UV-B in particular (Tevini and Teramura, 1989; Day and Neale, 2002) are documented to reduce net photosynthesis in leaves; however, $A_o$ was unaffected in all of our studies. Plant species would be expected to have effective repair mechanisms for their natural environment, and the moderate UV stress of 20 W m$^{-2}$ at 40°C did not exceed the repair capacity of plants, or cause irreversible damage.

In contrast, ‘Braeburn’ apple had reduced $F_v/F_m$ with no increase in $A_o$ at all sampling dates. Solovchenko and Schmitz-Eiberger (2003) also demonstrated that the shaded peel of ‘Braeburn’ had reduced $F_v/F_m$ with 11 W m$^{-2}$ of UV radiation at room temperature. We suggest that apple fruit peel, developed under the UV filter, did not induce UV repair mechanisms to the same extent as did the ambient control. This finding is supported by the reduced $F_v/F_m$ and increased $\Delta F/F_m$ on all three sampling dates in the UV filter treatment. However, in the presence of light, PSII and $A_o$ were unaffected by UV radiation (data not shown), suggesting that photosynthesis was able to supply the energy for UV repair mechanisms and the protection of PSII. Pfundel et al. (1992) demonstrated that UV-B effects were minimised by high PAR irradiation, and photo-reactivation was a key mechanism of DNA repair (Britt, 1996).

In contrast, the response of ‘Gala’ demonstrated a lack of $\Delta F/F_m$ except for the UV filter treatment, and increased $\Delta A_o$ with UV treatment. The ‘Gold Rush’ and ‘Granny Smith’ responses also demonstrated no impact on $\Delta F/F_m$, with an increase in $\Delta A_o$.

‘Braeburn’ is more susceptible to sunburn than the other cultivars (Evans, 2004) and was the only cultivar that did not respond to UV with increased $A_o$, but with increased $\Delta F/F_m$, indicating PSII damage. The $\Delta F/F_m$ and $A_o$ responses were not correlated with pigment content (data not shown), indicating that other processes were involved in their response to UV treatment.

The PF treatments had no effect on $F_v/F_m$, $A_o$, $\Delta F/F_m$, or $\Delta A_o$ in ‘Braeburn’ and ‘Gala’. We hypothesise that the particle film, which reflects UV radiation (Glenn et al., 2002), might prevent UV adaptation in the fruit.
However, removal of the PF before measurement indicates that UV adaptation was occurring, since its response was not significantly different from the control receiving ambient UV radiation, but significantly different from the UV filter treatment.

There was a pattern in all the apple studies. When the $\Delta F_{V}/F_{m}$ response to UV treatment was $< 0.02$, $\Delta A_0$ was generally $> 0.4 \mu \text{mol m}^{-2} \text{s}^{-1}$ indicating a significant increase in dark respiration. Conversely, when the $\Delta F_{V}/F_{m}$ response to UV treatment was $> 0.02$, then $\Delta A_0$ was $< 0.4 \mu \text{mol m}^{-2} \text{s}^{-1}$, indicating less stimulation of respiration (Figure 4). This pattern suggests that when UV repair mechanisms are effective, PSII is adequately protected with a $\Delta F_{V}/F_{m}$ of approx. 0, and protection occurs at the cost of higher respiration with $\Delta A_0 > 0.4 \mu \text{mol m}^{-2} \text{s}^{-1}$. However, when the UV repair mechanisms are ineffective, not only is PSII damaged and $\Delta F_{V}/F_{m} > 0.02$, but there is additional short-term damage to the repair mechanisms, indicated by a lack of respiration to provide energy. When fruit are not adapted to ambient UV levels, as in the UV filter treatments, there is greater damage to PSII, as measured by $\Delta F_{V}/F_{m}$ in the ‘Gala’ and ‘Braeburn’ studies. There was no significant correlation of $\Delta F_{V}/F_{m}$ or $\Delta A_0$ with any of the pigments evaluated over all studies (data not shown), suggesting that other mechanisms are interacting with pigment content in the response of peel to UV radiation.

The technique of measuring fruit peel gas exchange responses to environmental conditions provides new insights into fruit physiology. Therefore, when fruits are exposed to new radiation conditions associated with Summer pruning and/or re-orientation from fruit growth that could cause SI, successful adaptation may be predicted by examining both the $\Delta F_{V}/F_{m}$ and $\Delta A_0$ response.

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REFERENCES


UV effects on fruit surface physiology


