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Photosynthetically active radiation (PAR) × ultraviolet radiation (UV) interact to initiate solar injury in apple☆

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ABSTRACT

Solar injury (SI) in apple is associated with high temperature, high visible light and ultraviolet radiation (UV). Fruit surface temperature (FST) thresholds for SI related disorders have been developed but there are no thresholds established for solar radiation. The objective of the study was to measure the effect of different levels of FST, PAR and UV on quantum efficiency (Fv/Fm) alone and in combination to identify interactions affecting Fv/Fm recovery to serve as a guideline in evaluating SI-prevention technology. The variable transmission of UVb, UVa, PAR, and NIR through films of Surround™ and Raynox™ provided a wide range of radiation levels at the fruit surface to model Fv/Fm of photosystem II (PSII) in growth chamber and greenhouse studies. Increasing UV and PAR reduced Fv/Fm the greatest amount in 'Gala' while 'Granny Smith' had the least reduction suggesting that PSII in 'Granny Smith' has higher UV and PAR tolerance. All cultivars except 'Fuji' at harvest had some interaction component of PAR and UV that decreased Fv/Fm compared to untreated control fruit as both PAR and UV increased. When re-exposure was conducted on the 5 cultivars, Fv/Fm further decreased with the cumulative PAR and UV despite having a period of dark recovery between each 24 h exposure. Cultivar differences have a strong influence on the sensitivity of the peel to FST and radiation levels. Cultivars differ in their response to FST, UV and PAR as they mature and also exhibit year-to-year variation. This inconsistency suggests that acclimation to the environment also varies between years. PAR × UV interactions are complex and include the acclimation of the cultivar to the stress but in the prevention of SI, reducing FST, PAR and UV simultaneously is likely the most effective strategy.

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1. Introduction

Solar injury (SI) and sunburn in apple are associated with three environmental variables: high temperature, high PAR and ultraviolet radiation (as reviewed by Barber and Sharpe, 1971; Felicetti and Schrader, 2008; Glenn et al., 2002; Racsko and Schrader, 2012). SI is a broad term for solar-induced plant damage that may or may not indicate visual damage. Sunburn is defined as "damage to fruit by exposure to solar radiation" and "if the injury is mild, the flesh itself may not be damaged, but longer exposure can result in severe injury to both skin and flesh" (Jones and Aldinckle, 1990). Felicetti and Schrader (2008) and Schrader et al. (2001) described symptom development for the three types of sunburn in apple and the threshold fruit surface temperature (FST) associated with each type: 1) sunburn necrosis occurred at a FST of 52 °C, 2) sunburn browning occurred between FST of 46 °C and 49 °C in light, and 3) photooxidative sunburn occurred on non-acclimated tissue in the presence of moderate PAR levels with FST < 31 °C. Visually detecting SI and understanding the environmental conditions that occur at that time or immediately preceding visual symptoms do not necessarily reveal the underlying factor or factors that initiate metabolic or degradative processes leading to SI. Smillie and Hetherington (1983) initially proposed that *in vivo* chlorophyll fluorescence was a sensitive measure of stress tolerance and stress-induced injury in apple fruit. Chlorophyll fluorescence, and its various components, directly measure the performance of the aggregate chlorophyll content within the fruit tissue and are mechanistically associated with the plant's response to its environment via the non-radiative energy dissipation of fluorescence. Others (Seo et al., 2008; Song et al., 2001; Wand et al., 2008; Wűnsche et al., 2001) have subsequently confirmed that reductions in quantum efficiency (Fv/Fm) is a sensitive indicator of damage before and after visual SI symptoms have developed supporting the concept that damage to photoapparatus appears to be an early step in the development of SI (Barber and

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Sharpe, 1971; Rabinowitch et al., 1983). For example, Wand et al. (2008) demonstrated that Fv/Fm declined with each 2 h exposure of 'Cripps' Pink', 'Fuji', and 'Royal Gala' at FST's of 43 °C and that flesh browning developed after 8 to 12 hr of exposure and Wűnsche et al. (2001) found that 'Braeburn' fluorescence yield (Ft) was negatively and exponentially related to visual sunburn damage. Temperature thresholds leading to reduced Fv/Fm have been evaluated for several apple cultivars and demonstrated that FST < 40 °C generally do not reduce Fv/Fm but FST > 43 °C can result in a non-recoverable reduction in Fv/Fm in the absence of light (Chen et al., 2009; Song et al., 2001; Wand et al., 2008). While SI occurs in the presence of PAR and UV in the production setting, these studies are useful in defining the temperature thresholds of both fruit tissue and the chloroplast independently of radiation effects. Using polycarbonate filters to absorb UV radiation in field studies, Felicetti and Schrader (2008) found that PAR alone was the key factor linked to photooxidative sunburn in non-acclimated fruit and Glenn et al. (2008) demonstrated that the absence of UV did not affect apple peel Fv/Fm but did reduce carotenoid and anthocyanin pigments and reduced peel Fv/Fm when challenged with UV. UV treatment increased respiration in acclimated peel tissue but decreased Fv/Fm with no change in respiration in non-acclimated tissue (Glenn et al., 2008). SI often occurs when non-acclimated fruit are exposed to full sunlight due to summer pruning or fruit movement as fruit gains mass. Sun-exposed and shaded peel reacts differently to heat and solar radiation. High PAR exposure decreased 'Gala' shade peel Fv/Fm more than the acclimated and sun-exposed peel at FST of 31 °C (Li and Cheng, 2008). Similarly, in 'Fuji' peel, Fv/Fm decreased as FST increased from 25 °C to 44 °C but for FST > 46 °C there was little change. However, for FST > 46 °C, Fv/Fm was lower in the sun-exposed compared to the shaded peel indicating the capacity for electron transfer was damaged to a greater extent in the sun-exposed peel compared to the shaded peel (Chen et al., 2009). Ma and Cheng (2004) demonstrated that the apple peel Fv/Fm can recover from sudden exposure over a 10 day period. Pigment content also affects Fv/Fm response. Li and Cheng (2009) used a bud mutation, red 'Anjou', to compare the protective role of anthocyanins compared to the green 'Anjou' and demonstrated that for FST ≤ 42 °C FST and 0 PAR, Fv/Fm was unaffected by the mutation, however, for FST > 42 °C and high PAR Fv/Fm decreased more in the green 'Anjou' than the red 'Anjou indicating that elevated levels of anthocyanins play a protective role under conditions of high temperature and light. The role of PAR and UV in SI development appears to vary by the circumstances of the fruit prior to the exposure to extreme environmental conditions. The ability of apple fruit to recover from environmental stress (Glenn et al., 2008; Li and Cheng, 2009) indicates that in the production setting, apple can recover during the low light and night periods. However, if full recovery does not occur, a chronic condition may develop leading to reduced Fv/Fm and SI if the stress continues and exceeds biological thresholds.

Stress responses occur over a range of environmental factors and are expressed in some proportion to the stress factors in a continuum of response that, if taken to the extreme, results in cell, tissue or plant death. Soil and plant analysis have established threshold values to prevent visual symptom development and reduced productivity (Crassweller and Schupp, 2013; Ouimet et al., 2013) and threshold values of water stress can be established with spectral reflectance (Vertovec et al., 2001). Chlorophyll fluorescence is a key diagnostic tool in identifying early and asymptomatic nutrient deficiency (Kriedemann et al., 1985), heat, water and salinity stress (Sayed, 2003), ozone damage (Gielen et al., 2007) and disease development (Chaerle et al., 2004, 2006). The objectives of the present study were to 1) use PAR and UV filters to develop a range of PAR and UV levels that lead to reduced Fv/Fm in apple peel, 2) identify levels of FST, PAR and UV that exceed the ability of five apple cultivars to fully recover after 24 h, 3) measure the effect of varying levels of FST, PAR and UV on Fv/Fm alone and in combination to identify interactions affecting Fv/Fm in recovery as guidance in evaluating SI prevention technology.

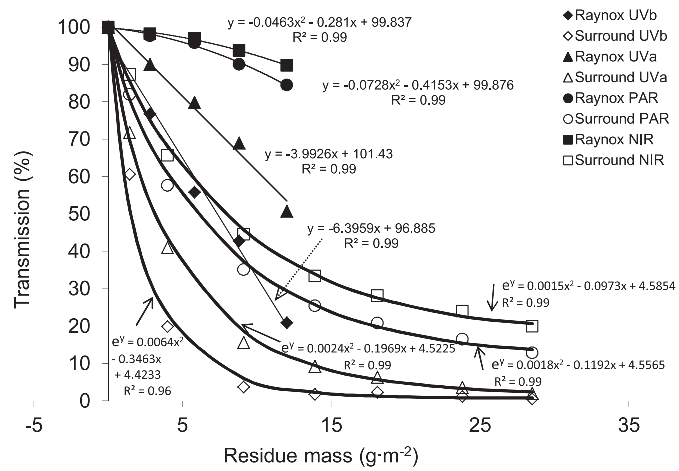

Fig. 1. Transmission of ultraviolet b (UVb, 280–320 nm), ultraviolet a (UVa, 320–400 nm), photosynthetically active radiation (PAR, 400–700 nm), and near infrared radiation (NIR, 700–1100 nm) through Raynox™ and Surround™ for a range of residue levels.

2. Materials and methods

2.1. Determination of residue amounts and radiation transmission

Treatments of Surround™ WP (NovaSource, Phoenix, AZ) and Raynox™ (35% solids, Pace, Inc. Seattle, WA) were prepared at 3% and 0.3%, w/w and v/v, respectively. Surround™ WP is based on kaolin, a white, non-porous, non-swelling, low-abrasive, fine grained, plate-shaped, aluminosilicate mineral ($Al_4Si_4O_{10}(OH)_8$) that easily disperses in water and is chemically inert over a wide pH range. Raynox™ is a suspension of carnauba wax, organically modified clay and emulsifiers. The materials were sprayed on to quartz slides with a sprayer that produced a thin and uniform film. Sequential applications were made to develop a range of residue from 0 to 25 g m^{-2} of Surround™ and 0 to 8 g m^{-2} of Raynox™. Transmission of UVb (280–320 nm), UVa (320–400 nm), PAR (400–700) and NIR (700–1100 nm) was measured with a StellarNet spectral radiometer (StellarNet, Tampa FL. Model EPP 2000). Residue amounts on the quartz slides were measured by weight reduction of the slides after cleaning (Fig. 1 and Table 1). Residue amounts of 12 µl droplets containing 3% and 0.3% Surround™ and Raynox™ were measured by measuring the weight reduction of 10 dried droplets placed on a slide (Table 1).

2.2. Plant material

'Gala', 'Braeburn', 'Fuji', 'Granny Smith' and 'Cripps' Pink' were collected from 7 to 10-year-old-trees managed with standard pest management practices at the USDA-ARS-Appalachian Fruit Research Station, Kearneysville, WV. Fruit were collected approximately 30 days before maturity and at maturity. Maturity was based on industry firmness and soluble solids content of 30 fruit. Selected fruit were collected from the interior of the tree canopy. Prior to each experiment, fruit were collected at 1600 to 1700 HR and the study performed the following morning. Fruit were stored at room temperature in the dark prior to the experiment to simulate the

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