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## The role of solar UV in long-term adaptation of ripening apple fruits to high sunlight

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(Received February 3, 2005)

### Summary

The changes in chlorophyll, carotenoid and quercetin glycoside content were studied in two apple (*Malus domestica* Borkh.) varieties, Braeburn and Granny Smith, with different ability for acclimation to sunlight, during their on-tree ripening under full-spectrum solar radiation and without UV component. Exclusion of solar UV did not affect the development of the variety-specific patterns of photosynthetic pigments during fruit ripening and adaptation to the visible solar radiation. On the contrary, solar UV was crucial for the accumulation of quercetin glycosides, the main group of phenolics serving for UV acclimation in apple fruits. High content of quercetin glycosides (QG) was maintained in the sunlit skin of fruits grown with solar UV in the course of ripening. Apart from solar UV-inducible QG in sunlit skin, there was a 'background' level of these compounds in the shaded skin that was not affected by solar UV. The QG of shaded apple skin presumably originate from constitutive phenolic metabolism and may serve for protection against diffuse UV of sunlight scattered by canopy.

### Introduction

Although the energy of solar radiation is required by green plants to drive photosynthesis, it could be harmful when absorbed in amounts higher than could be utilised by photosynthetic apparatus (ASADA, 1994; NIYOGI, 1999). Additionally, under natural conditions plants are inevitably exposed to UV radiation, the obligatory component of solar spectrum (CALDWELL, 1981; CALDWELL et al., 1998). Harmful effects of excessive fluxes of visible radiation are mediated by reactive oxygen species (ROS) and excited states of chlorophyll (NIYOGI, 1999). High-energy UV, especially UV B (280-315 nm) quanta are efficiently absorbed by and cause direct and ROS-mediated damages to nucleic acids, proteins, lipids and pigments (BORNMAN et al., 1997; COCKELL and KNOWLAND, 1999). However, environmental fluxes of solar radiation rarely cause significant damage to plants due to operation of photoprotective mechanisms based on sunlight avoidance, dissipation of the excessive absorbed energy, elimination of ROS and reparation of damaged molecules (NIYOGI, 1999).

Under prolonged exposure to high fluxes of solar radiation which is likely to occur in nature, screening and rearrangement of pigment apparatus gain an increased importance as photoadaptive mechanisms (HAVAUX and KLOPPSTECH, 2001). Long-term photoadaptation involves a decrease in chlorophyll (Chl) content, especially Chl *b*, as a result of the adjustment of light-harvesting antenna (NIYOGI, 1999) and an increase in carotenoids (Car) serving for dissipating of excessive energy (YOUNG and FRANK, 1996), ROS quenching (YOUNG, 1991) and, in some cases, trapping of blue light (MERZLYAK and SOLOVCHENKO, 2002). In higher plants, internal sunscreens are formed of phenolic compounds which selectively absorb radiation in the visible and/or UV regions of the spectrum (CALDWELL et al., 1983), such as

anthocyanins, flavonols and phenolic acids (COCKELL and KNOWLAND, 1999) and accumulated in superficial structures of leaves and fruits (BAUR et al., 1998; CALDWELL et al., 1983; SOLOVCHENKO and MERZLYAK, 2003; MERZLYAK et al., 2004).

Acclimation to high sunlight appears to be a complex process involving mechanisms protecting against both the visible and UV components of the solar spectrum (CEROVIC et al., 2002; MERZLYAK et al., 2002). Adaptation to elevated UVB radiation results, apart from the build-up of phenolic sunscreens, in alterations of photosynthetic pigment and antioxidant content (TEVINI and TERAMURA, 1989) which may induce cross-resistance to damage by strong visible radiation (HAVAUX and KLOPPSTECH, 2001) and oxidative stress (KONDO and KAWASHIMA, 2000). Thus, in sun-adapted apple fruits with high flavonol content, Chl and Car were more resistant to bleaching by strong visible radiation than in shade-adapted (in preparation).

Complex nature of solar radiation imposes difficulties in the estimation of the role of its visible and UV components in the expression of particular responses involved in long-term adaptation in plants. Previous studies (LINGAKUMAR et al., 1999) showed the necessity of a control without UV to study the realistic effects of UV radiation; therefore we employed exclusion of solar UV in the field. Our experiments were carried out on apple fruits since they represent a unique natural system for investigation of photoadaptation and photoprotection in plants, combining both sunlight-affected (sunlit) and shaded tissues within a single fruit (ANDREWS and JOHNSON, 1997; SCHMITZ-EIBERGER and NOGA, 2001; MERZLYAK et al., 2002). Previously we established that the strategy of adaptation of apples to high sunlight comprises a decrease in Chl, retention or accumulation of Car and a build up of phenolic compounds in the fruit skin (MERZLYAK et al., 2002). Flavonoids are the major group of apple skin phenolics (ESCARPA and GONZÁLEZ, 1998) represented mainly by quercetin glycosides (QG) and anthocyanins (AWAD et al., 2001), readily induced by strong sunlight (SOLOVCHENKO and SCHMITZ-EIBERGER, 2003; MERZLYAK et al., 2004); other apple phenolics (catechin and phenolic acid) display little or no correlation with solar irradiance (AWAD et al., 2001). The goal of the present study was to find out whether the normal levels of solar UV affect the expression of the photoadaptive responses in ripening apple fruits. To the best of our knowledge, this is the first report about long-term effects of UV exclusion in fruits. These data should improve our understanding of mechanisms and possible ways to control photo-oxidative damages of fruits such as sunburn and postharvest diseases of apples.

### Materials and methods

#### Plant material

Two apple (*Malus domestica* Borkh.) varieties, Granny Smith and Braeburn, differing in their ability for acclimation to strong sunlight were involved in the investigation. The fruits were grown on Klein-Altendorf Fruit Research Station (Germany). Some fruits were grown

### Abbreviations

Car, carotenoids; Chl, chlorophyll(s); QG, quercetin glycosides.

in cone-shaped bags made of 'Folitec UV-5' ('Agrarfolien-Vertriebs GmbH', Westerburg, Germany), which absorb UVB and nearly all UVA radiation but did not significantly attenuate PAR (Fig. 1). Holes were provided in the bags preventing unfiltered solar light from getting inside and maintaining atmosphere and temperature similar to ambient. Other fruits were exposed to unaltered solar radiation. These fruits comprised '-UV' and '+UV' variants, respectively. In order to simplify the experimental design, we used fruits low anthocyanin content in this experiment.

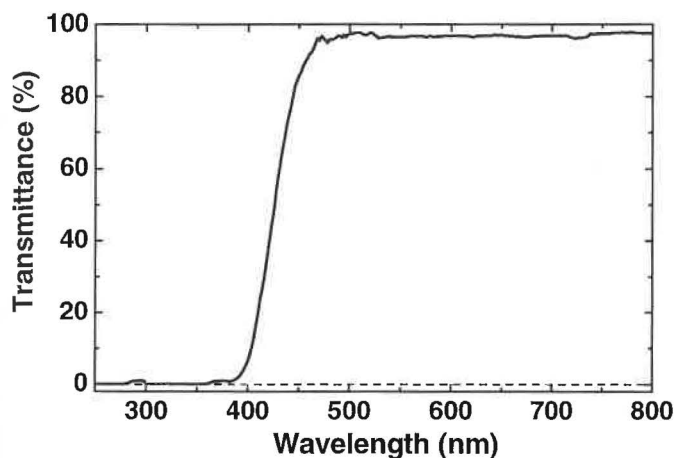


Fig. 1: Transmittance spectrum of the UV-absorbing film used for bagging the fruits.

Sampling was started when the fruits were expanded to the size suitable for the measurements. Five undamaged fruits of each variety were randomly picked each two weeks over a period from 7.08.2003 to 17.09.2003 and studied within 24 h. All analyses were performed both on sun-exposed and shaded sides of each fruit, which were discerned visually. Small regions of the fruit surface (ca. 4 cm<sup>2</sup>) were selected, which were enough to perform reliable measurement of pigment content (MERZLYAK and SOLOVCHENKO, 2002).

#### Natural UV irradiance

The data on daily global UV irradiance (Fig. 2) at the experimental site were obtained from meteorological monitoring laboratory of Max Planck Institute (Cologne, Germany).

#### Pigment analysis

Extraction procedure allowing simultaneous assay of Chl, Car, QG and was employed according to SOLOVCHENKO et al. (2001). The check anthocyanin presence was accomplished by acidification of water-methanol phase of the extract by HCl and measuring absorbance at 530 nm. Separation and identification of flavonoids was carried out by HPLC as described previously (SOLOVCHENKO and SCHMITZ-EIBERGER, 2003).

#### Statistical treatment

Data were statistically analysed employing two-factor ANOVA from data analysis tools of Microsoft Excel spreadsheet software (Redmond, USA).

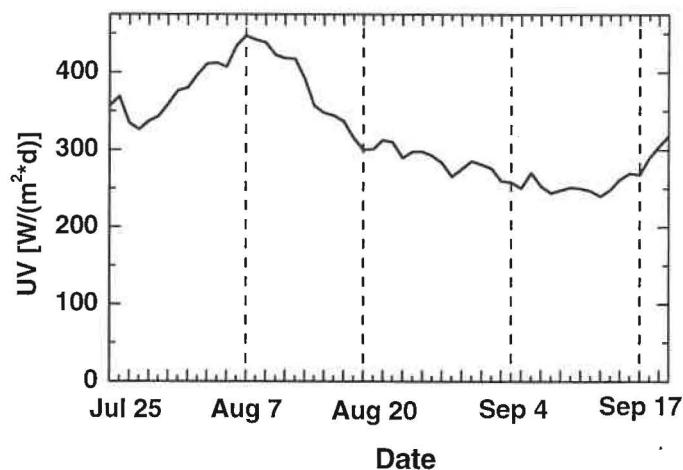


Fig. 2: Daily UV irradiance at the experimental site (Klein-Altendorf Research Station, Bonn University). The sampling dates are indicated by dashed lines.

## Results

### 1. Photosynthetic pigment content

Content of Chl, Car and QG as well as Car to Chl ratio of sunlit and shaded skin were monitored in fruits of both varieties during their on-tree ripening in the presence ('+UV') and in the absence ('-UV') of solar UV (Figs. 3-6). Regardless of the presence of solar UV, content of Chl increased in both varieties until the end of August when the fruits continued to expand and started to decline by the beginning of September evidencing the onset of ripening (Figs. 3 and 4). In Braeburn, degradation of Chl on the background of Car retention led to an increase of Car/Chl ratio which was sharper on the sunlit side (Figs. 3C, D). Granny Smith showed a little change in Car/Chl ratio due to more or less synchronous changes of Car and Chl content (Figs. 4C, D). As a result, Braeburn fruits turned yellowish whereas fruits of Granny Smith remained green in color until advanced stages of ripening.

In Braeburn, no significant difference in Chl content was found between '+UV' and '-UV' variants whereas the skin of sunlit side possessed lower Chl content than shaded in both variants (Figs. 3A, B). On an average, Granny Smith had 2-3 times higher Chl content but Chl content in sunlit skin of Granny Smith did not differ significantly from the shaded skin of this variety or was higher (Figs. 4A, B). The '-UV' fruits of Granny Smith often had lower Chl content in sunlit and shaded skin than the '+UV' fruits of the same variety (cf. Figs. 4A and 4B).

Sunlit skin of Braeburn fruits possessed higher Car content than the shaded skin in the '+UV' and '-UV' variants (not shown). Accordingly, Car/Chl ratio was higher on the sunlit sides of these fruits (Figs. 3C, D). The Car/Chl ratio showed a gradual increase in the course of ripening. The increase was sharper on sunlit side (Figs. 3C, D; open bars), therefore the gap in Car/Chl between sunlit and shaded skin tended to increase as the ripening proceeded. The velocity of the increase in Car/Chl ratio was higher in the fruits grown under full sunlight, but the difference became significant only when fruits ripened (cf. Figs. 3C and 3D).

Sunlit and shaded skin of Granny Smith did not differ significantly in Car content; Car content varied synchronously with that of Chl and was higher in the '+UV' variant (not shown). Fruits of this variety possessed close Car/Chl ratios on sunlit and shaded sides which did not change considerably in the course of ripening (Figs. 4C, D). The fruits harvested on August and later had a little but statistically significant increase in Car/Chl ratio on the sunlit side (Figs. 4C, D).

Generally, Car/Chl ratio was higher on sunlit side both in '+UV' and '-UV' variants but the difference was much lower in comparison with ripe fruits of Braeburn (cf. Figs. 3C, D and 4C, D).

## 2. Quercetin glycoside content

In all experimental variants QG content reached the maximum at the third decade of August, then by the beginning of September it declined to the level recorded at the beginning of August and did not change significantly until the end of the observation period (Figs. 5 and 6). The highest QG content was found in sunlit skin of the '+UV' Braeburn fruits; in the shaded skin of these fruits QG content was 2-3 times lower (Fig. 5A). The '-UV' fruits of this variety possessed remarkably lower QG content in sunlit skin in comparison with the '+UV' fruits (Fig. 5B); it did not differ from QG content of shaded skin of fruits both in '+UV' and '-UV' variants [except fruits harvested on August, 20] (cf. Figs. 5A and 5B).

Sunlit and shaded skin of Granny Smith fruits grown in the presence of solar UV displayed the same pattern of QG content as Braeburn but contained 2-2.5 times lower amounts of QG (Figs. 5A and 6A).

Like Braeburn, sunlit skin of Granny Smith fruits in the '-UV' variant possessed a reduced QG content in comparison with the '+UV' variant, whereas shaded peel displayed almost no difference in QG content between the '+UV' and '-UV' variants (Figs. 6A and 6B).

## Discussion

In this work we studied fruits of two apple varieties, Braeburn and Granny Smith, differing in their ability to acclimate to sunlight, ripening under unaltered sunlight and without solar UV. The results showed that exclusion of solar UV exerted no or little effect on variety-specific patterns of pigment changes during ripening. Regardless of the UV presence, both varieties displayed a decline in Chl content (Figs. 3A, B and 4A, B); ripening of Braeburn was accompanied by a considerable increase in Car/Chl ratio (Figs. 3C, D), which was not the case in Granny Smith (Figs. 4C, D).

Apart from traits characteristic of ripening, pigment patterns of the studied fruits possessed features attributable to sunlight acclimation. Thus, Braeburn fruits showed a distinct high-light response expressed as a decrease of Chl (Figs. 3A, B), an increase in Car content (not shown), and higher Car/Chl ratio (Figs. 3C, D) in sunlit skin in comparison with shaded skin within the same variant. This kind of response was recorded in the fruits grown with (Figs. 3A, C) and

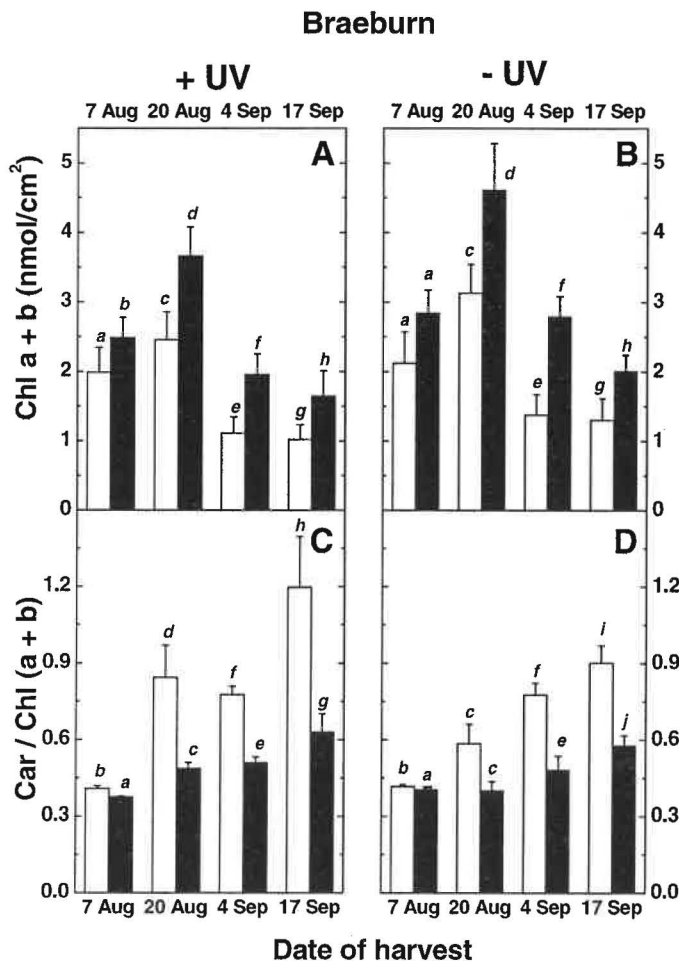


Fig. 3: Changes in chlorophyll content (A, B) and carotenoid to chlorophyll ratio (C, D) of sunlit (open bars) and shaded (closed bars) skin of ripening Braeburn fruits grown under unaltered sunlight (A, C) and with UV filtered out (B, D).

In this and the other figures, results are means of four to six replicates; standard errors are indicated as bars. For each variable dissimilar letters after means indicate statistically different ( $P > 0.05$ ) groups according to two-way ANOVA results.

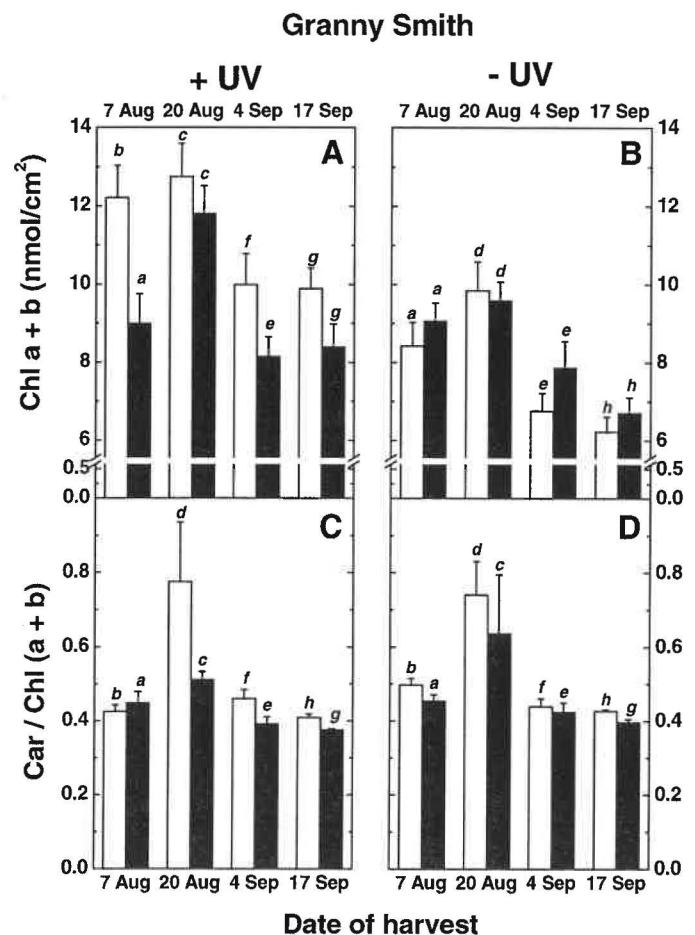


Fig. 4: Changes in chlorophyll content (A, B) and carotenoid to chlorophyll ratio (C, D) of sunlit (open bars) and shaded (closed bars) skin of ripening Granny Smith fruits grown under unaltered sunlight (A, C) and with UV filtered out (B, D).

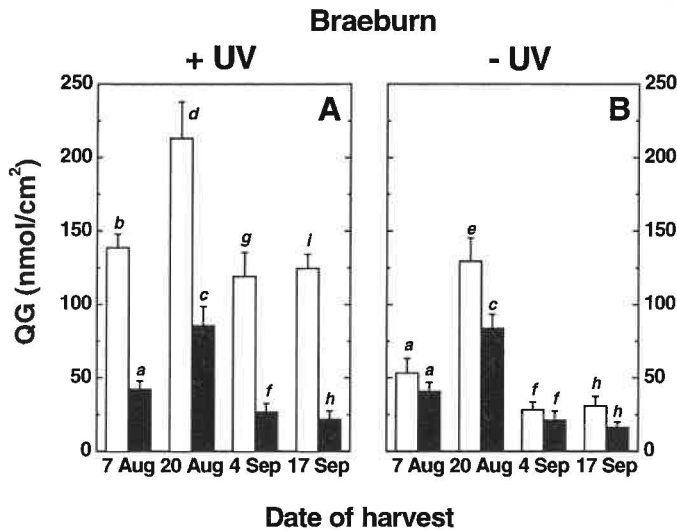


Fig. 5: Changes in quercetin glycoside content of sunlit (open bars) and shaded (closed bars) skin of ripening Braeburn fruits grown under unaltered sunlight (A) and with UV filtered out (B).

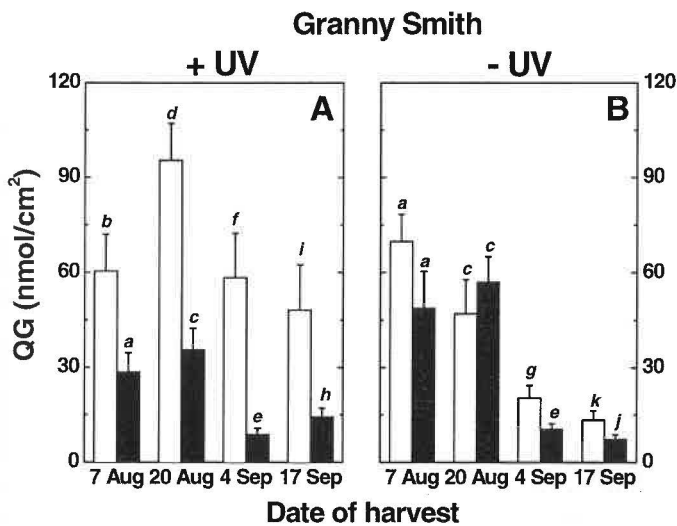


Fig. 6: Changes in quercetin glycoside content of sunlit (open bars) and shaded (closed bars) skin of ripening Granny Smith fruits grown under unaltered sunlight (A) and with UV filtered out (B).

without solar UV (Figs. 3B, D). Fruits of Granny Smith possessed a weak response to strong sunlight showing no or little changes in pigment content that could be specifically related with solar irradiance (Fig. 4). This is in accord with our previous studies where this variety was found to have a limited ability of photoadaptation proposed as possible reasons of its susceptibility to photooxidative damage, such as sunburn (MERZLYAK et al., 2002). Collectively, obtained results suggest that the UV component of solar radiation does not seem to be necessary or accounts for the development of pigment patterns characteristic of ripening or adaptation to strong sunlight.

In addition to rearrangement of photosynthetic pigments, a build-up of flavonoids, including QG that occurs in vacuoles of skin cells belongs to general high-sunlight responses of plants (CALDWELL et al., 1983; BORNMAN et al., 1997; MERZLYAK et al., 2004). This type of response was detected in sunlit skin of all apple fruits grown under unaltered sunlight regardless of cultivar but was more

pronounced in Braeburn than in Granny Smith (Figs. 5A and 6A); by contrast, in fruits grown with solar UV filtered off, the QG content of sunlit skin was almost the same as in the shaded skin (Figs. 5B and 6B).

Interestingly, in Granny Smith '- UV' content of Chl was significantly lower than in '+UV' fruits of the same variety. According to HAVAUX and KLOPPSTECH (2001), flavonoids are able to exert a strong protective effect against radiation in the blue part of the visible spectrum, this additional protection might be important in the case of fruits with high Chl content like Granny Smith. This hypothesis is compatible with our data on *in vivo* optical properties and concentration of apple skin QG suggesting that the role of QG in photo-protection might be more significant than expected from the *in vitro* spectra. Taking this into account, the low QG content of Granny Smith grown without UV might render it vulnerable even to normal fluxes of solar radiation and lead to a decrease in Chl. We can note in addition, that phenolic compounds accumulated during on-tree ripening of apple fruits are related with resistance to postharvest diseases such as superficial scald (JU and BRAMLAGE, 1999). Therefore the levels of solar UV might have relevance to the extension of fruit life in storage.

Surprisingly, the exclusion of solar UV did not lead to a decrease of QG in shaded apple skin. Moreover, in '-UV' fruits QG content of sunlit skin kept at the level recorded in shaded skin (Figs. 5B, D and 6B, D). Similar retention of flavonoids after exclusion of UV was found in leaves of other higher plant species (LINGAKUMAR et al., 1999; TURUNEN et al., 1999). There is probably a threshold, under which the concentration of the UV absorbing compounds in the protective tissues is not furthermore reduced, in spite of the low levels of the stressor (UV radiation) in the environment (LIAKOURA et al., 2003). This threshold might arise due to constitutive phenolic metabolism and could explain substantial accumulation of QG in shaded apple skin and in the absence of UV. These QG may serve for protection against diffuse UV which comprises significant part of solar light scattered by canopies (PARISI et al., 2000).

## Conclusions

Summarizing the results of this work, we can conclude that the presence of ambient levels of solar UV does not exert a notable effect on Chl and Car changes involved in long-term acclimation to the visible solar radiation, at least in apple fruits (Figs. 3 and 4). On the contrary, solar UV was crucial for the induction of an important UV-protecting mechanism in apples – accumulation of UV-absorbing QG in the skin (Figs. 5 and 6). Throughout ripening, skin QG content followed the UV irradiation trend (cf. Figs. 2, 5, and 6) and was maintained in sun-exposed skin at the level sufficient for protection against UV-induced damage (SOLOVCHENKO and SCHMITZ-EIBERGER, 2003). Apart from solar UV-inducible QG in sunlit skin, there was a more or less constant 'background' level of these compounds in shaded skin that was not affected by solar UV and could serve presumably for protection against diffuse UV (PARISI et al., 2000).

## Acknowledgements

The authors are grateful to Prof. M.N. Merzlyak for his useful notes and critical reading of the manuscript.

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