Continuous UV-B Irradiation Induces Endoreduplication and Trichome Formation in Cotyledons, and Reduces Epidermal Cell Division and Expansion in the First Leaves of Pumpkin Seedlings (Cucurbita maxima Duch. × C. moschata Duch.)

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(Received April 24, 2014; Accepted July 24, 2014)

We examined the effects of continuous ultraviolet-B (UV-B) irradiation (0.58 W m⁻²) for 15 d on pumpkin seedlings. Continuous irradiation for 15 d slightly reduced the expansion of epidermal cell area and leaf area, whereas total epidermal cell number did not change in cotyledons. Only normal trichomes consisting of three cells were observed on the surface of control cotyledons. On the UV-B-irradiated cotyledon surface from 3-7 d, smaller trichomes consisting of single cells were observed along with normal trichomes. The total number of trichomes increased after UV-B irradiation for 5-9 d compared with that of control cotyledons. Expansion of true leaves was disrupted by UV-B irradiation for 15 d. Expansion of epidermal cell area and leaf area was reduced substantially, and the total number of epidermal cells was reduced considerably after UV-B irradiation for 15 d. Thus, continuous UV-B irradiation of pumpkin seedlings induces endoreduplication and trichome formation in tissues lacking active cell division (cotyledons), and reduces cell division in tissues that are actively growing (shoot apical meristem including first leaves).

Keywords : shoot apical meristem (SAM)

INTRODUCTION

Ultraviolet-B (UV-B; 280–320 nm) irradiation has pleiotropic effects on development, morphology, and physiology of higher plants (Frohnmeyer and Staiger, 2003). Exposure to UV-B causes DNA and membrane damage, reduced photosynthetic activity, inhibition of hypocotyl elongation, stunted growth, reduced leaf area, bronzing, and necrosis (Teramura, 1983; Ziska et al., 1992; Krizek et al., 1993; Teramura and Sullivan, 1994). Thus, UV-B irradiation inhibits plant growth.

Plant growth is driven by cell division coupled with subsequent elongation and differentiation of the daughter cells (Beemster et al., 2003; Jakoby and Schnittger, 2004). Cell division plays a role in developmental processes that create plant architecture and in modulating plant growth rate in response to environmental conditions (Cockcroft et al., 2000; Beemster et al., 2002). In higher plants, the shoot apical meristem (SAM) and root apical meristem (RAM) are the tissues with active cell division. In other tissues that lack active cell division, cells can sometimes undergo endoreduplication, an alternative cell cycle process in which DNA replication continues without mitosis or cytokinesis (Nagl, 1976; Barlow, 1978). Endoreduplication in higher plants often occurs during cell elongation and differentiation, and some have suggested that it could play an important role in cell-size regulation (Traas et al., 1998). The DNA content of endoreduplicated nuclei is much greater than 2 C (C is the haploid DNA content). For example, trichomes are generated by endoreduplication of epidermal cells. Arabidopsis trichomes consist of single cells that emerge from the epidermis of leaves and stems. The single trichome nucleus continues to replicate its genomic DNA during differentiation, reaching levels of 20–32 C (Melaragno et al., 1993; Hulskamp et al., 1994). The surface of cucumber (Cucumis sativus L.) cotyledons contains trichomes composed of three cells with nuclear DNA levels of 6.7–8.2 C, which is greater than that in epidermal cells (Yamasaki et al., 2010). Cell division and endoreduplication are important processes for plant growth.

Aerial parts of pumpkin (Cucurbita maxima Duch. × C. moschata Duch.) seedlings contain the cotyledons, hypocotyl, and SAM. Although cell division is active in the SAM, it does not occur in open cotyledons. Therefore, pumpkin seedlings represent an excellent system to study the effects of UV-B irradiation on tissues with and without active cell division. To clarify the effects of UV-B irradiation on higher plants over short-term periods, an experimental system designed to provide continuous UV-B irradiation at intensities that do not cause severe damage to the plants is useful. We previously showed that continuous UV-B irradiation (0.57 W m⁻²) of cucumber (Cucumis sativus L.) seedlings induced endoreduplication, caused rapid expansion of the epidermal cells surrounding trichomes in cotyledons (Yamasaki et al., 2007; 2010), and reduced epidermal cell division and expansion in true leaves (Yamasaki et al., 2014). The effects of continuous
UV-B irradiation on seedlings of other species was unknown. This knowledge would broaden the understanding of UV-B irradiation in higher plants. In the present study, we exposed pumpkin seedlings to UV-B irradiation (0.58 W m\(^{-2}\)) for 15 d to examine the effects of continuous irradiation on cotyledons and SAM. We observed morphological changes in the seedlings and measured the epidermal cell area and total epidermal cell number in both cotyledons and first leaves. We also measured the total number of trichomes on cotyledons. This paper discusses the effects of continuous UV-B irradiation on cotyledons and SAM of pumpkin seedlings at morphological and cytological levels, and compares these results with those obtained from cucumber seedlings.

**MATERIALS AND METHODS**

*Plant materials*

Pumpkin (*Cucurbita maxima* Duch. × *C. moschata* Duch. cv. Shin-tosa) seeds were purchased from Nakahara Seed Co., Ltd. (Fukuoka, Japan). Seeds were germinated on wet filter paper in a Petri dish at 26°C in the dark for 2 to 3 d, and seedlings were transferred to plastic pots containing the soil composite Kumiai-Engei-Baido (0.4 g of N, 1.2 g of P, 0.2 g of K per kg; Seishin Sangyo Co., Ltd., Kitakyushu, Japan). The plants were grown under continuous fluorescent light (FLR40SW/M/36-B; Hitachi, Ltd., Tokyo, Japan) in an incubator (LH-200RDS; Nihon Ikakikai Co., Ltd., Osaka, Japan) at 26°C. The photosynthetic photon flux density (PPFD) at the plant surface was approximately 213 \(\mu\)mol m\(^{-2}\) s\(^{-1}\).

**UV-B irradiation**

The method for UV-B (280–320 nm) irradiation was essentially the same as that described in Yamasaki et al. (2007). When the cotyledon blades were approximately 3.0 cm long, plants were transferred to a growth cabinet furnished with continuous fluorescent light (FLR40SW/M36-B; Hitachi, Ltd., Tokyo, Japan) at 25°C, with a PPFD at the plant surface of approximately 160 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). For continuous UV-B irradiation, a sunlamp (FL-20E; Tozai Duch., Ltd., Osaka, Japan) was suspended 7 cm above the plant surface of approximately 160 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). The UV intensity was measured using digital UV intensity meters (UV-5.7, UV-6.2, and UV-8.0; MK Scientific, Inc., Yokohama, Japan). The intensities are summarized in Table 1. The average intensity of UV-B irradiation was 0.58 ± 0.03 W m\(^{-2}\). The UV-A intensity was 0.34 ± 0.02 W m\(^{-2}\) for control plants and 0.38 ± 0.02 W m\(^{-2}\) for UV-B-irradiated plants. Because the UV-A intensities were similar in the treatment and control groups, the effects of UV-A irradiation were not considered in the present study.

*Observation of pumpkin seedlings*

To investigate the effects of continuous UV-B irradiation on pumpkin seedlings, the pumpkin seedlings were photographed with a digital camera (Power shot A95; Canon, Inc., Tokyo, Japan) under the same conditions of lightning and angle after UV-B irradiation for 0, 3, 7, 11, and 15 d.

*Measurement of leaf area and epidermal cell area in cotyledons and first leaves*

Cotyledons and unfolded first leaves were excised with a razor blade after UV-B irradiation for 0, 3, 7, 11, and 15 d, and the leaf areas were calculated using “photomeasure” software (Kenis, Ltd., Osaka, Japan). Six cotyledons (n = 6, one cotyledon per plant) and the five first leaves of the six plants were used to calculate the average leaf area at 0, 3, 7, 11, and 15 d. Thus, a total of 60 plants were used. In the same samples, the average area of 60 epidermal cells from six cotyledons (ten epidermal cells per cotyledon) and the average area of 50 epidermal cells from five first leaves (ten epidermal cells per first leaf) were calculated using the “photomeasure” software. Before measuring the epidermal cell areas in cotyledons and first leaves, samples were treated with 10% (w/v) potassium hydroxide (KOH) until they were decolorized, and then stained with 0.005% toluidine blue O for 1 h at room temperature. Toluidine blue O stains polyphenolic compounds in higher plants (Ros Barcelo et al., 1989; Yamasaki et al., 2007).

*Calculation of total epidermal cell number in cotyledons and first leaves*

The same samples described above were used to calculate total epidermal cell number in cotyledons and first leaves. Total epidermal cell number in one cotyledon was calculated by dividing the leaf area by the average area of ten epidermal cells in each cotyledon. Then, average of the total epidermal cell number in the six cotyledons was calculated. Total epidermal cell number in one first leaf was calculated by dividing the leaf area by the average area of ten epidermal cells in each first leaf. Then, average of the

**Table 1** Intensity of UV received by the control and the UV-B-irradiated pumpkin cotyledons. The UV intensity of a sunlamp without films is given for comparison. All UV intensities were measured 7 cm below the sunlamp.

<table>
<thead>
<tr>
<th>Intensity of UV</th>
<th>UV-C (W m(^{-2})) (246–262 nm)</th>
<th>UV-B (W m(^{-2})) (280–320 nm)</th>
<th>UV-A (W m(^{-2})) (320–400 nm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunlamp</td>
<td>N.D.(^a)</td>
<td>2.67(^b)</td>
<td>0.74(^c)</td>
</tr>
<tr>
<td>Sunlamp + polyester film (control)</td>
<td>N.D.(^a)</td>
<td>N.D.(^a)</td>
<td>0.34 ± 0.02(^y)</td>
</tr>
<tr>
<td>Sunlamp + polyvinyl chloride film (UV-B-irradiated)</td>
<td>N.D.(^a)</td>
<td>0.58 ± 0.03(^y)</td>
<td>0.38 ± 0.02(^y)</td>
</tr>
</tbody>
</table>

\(^a\) N.D., not detected.

\(^b\) Values represent the means ± standard error at three different places for 7 d.
UVB EFFECTS ON PUMPKIN SEEDLINGS

Fig. 1 Scheme of ten points where trichome density was investigated in pumpkin cotyledons. To calculate total trichome number, trichome number and leaf area in the field-of-view of a 100× objective were analyzed under a light microscope at each point per cotyledon. Four cotyledons (n=4, one cotyledon per plant) were used to calculate the total trichome number at 0, 1, 3, 5, 7, 9, 11, 13, and 15 d.

Observation of cotyledons

To investigate the effect of UV-B irradiation on trichomes in pumpkin cotyledons, cotyledons irradiated with UV-B for 3, 7, 11, and 15 d were excised, decolorized, and stained with toluidine blue O as described above, and observed under a light microscope. To measure the DNA content of the adaxial epidermal cells and trichomes in pumpkin cotyledons, a cytophotometric method described by Szymanski and Marks (1998) was used. Cotyledons of control plants at 0 d were excised and treated with 20% (w/v) ethanol at room temperature for 20 h. After cotyledons were immersed in phosphate-buffered saline (PBS; 136.7 mM NaCl, 2.7 mM KCl, 8.1 mM Na2HPO4,

Fig. 3 Effects of 15 d continuous UV-B irradiation on (A) leaf area, (B) epidermal cell area, and (C) total epidermal cell number (C) in pumpkin cotyledons. Six cotyledons (n=6, one cotyledon per plant) were used to calculate the average leaf area at 0, 3, 7, 11, and 15 d. Epidermal cell area is expressed as the average of 60 measurements of epidermal cell area from six cotyledons (ten epidermal cell area measurements per cotyledon). Total epidermal cell number in each cotyledon was calculated by counting epidermal cell number in six cotyledons, with 60 epidermal cell samples measured per cotyledon. The effects of 15 d continuous UV-B irradiation on (D) leaf area, (E) epidermal cell area, and (F) total epidermal cell number in pumpkin first leaves. Five first leaves of the six plants were used to calculate the average leaf area at 0, 3, 7, 11, and 15 d. Epidermal cell area is expressed as the average of 50 measurements of epidermal cell area from the five first leaves (ten epidermal cell area measurements per first leaf). Total epidermal cell number in each first leaf was calculated by counting epidermal cell number in five first leaves, with 50 epidermal cell samples measured per first leaf. Bars indicate ± standard error. Single asterisk indicates a difference between control and UV-B-irradiated cotyledons (P<0.05, Student’s t-test). Double asterisk indicates a significant difference between control and UV-B-irradiated cotyledons (P<0.01, Student’s t-test).
and 1.5 mM KH$_2$PO$_4$) for 10 min, DNA was stained with 4',6-diamidino-2-phenylindole (DAPI) at a concentration of 2 µg ml$^{-1}$ for 30 min. Cotyledons were then washed three times with PBS and once with distilled water. Stained DNA was visualized by fluorescence microscopy (ECLIPSE E600W; Nikon, Co., Tokyo, Japan) equipped with a UV-2A filter (excitation: 330–380 nm, emission: 420 nm), and photographed with a digital camera (Power Shot A95; Canon, Inc., Tokyo, Japan). Thirty nuclei in cotyledons were counted. Digital images were converted to a grey scale using Adobe Photoshop 7.0. The fluorescence output of individual nuclei was analyzed with the public-domain NIH Image program (http://rsb.info.nih.gov/nih-image/) using a protocol similar to that of Szymanski and Marks (1998). The intensity of 30 guard-cell nuclei in five fields-of-view of one sample under light microscopy (100× objective) was used as an internal standard that indicated a relative DNA content of 2 C.

Calculation of total trichome number in cotyledons

Before calculating total trichome number in pumpkin cotyledons, the average trichome density at ten points of a cotyledon (Fig. 1) was calculated using the trichome number, the leaf area in the field-of-view of a 100× objective under a light microscope, and the “photomeasure” software (Kenis, Ltd., Osaka, Japan). The total trichome number in cotyledons was calculated by multiplying trichome density by cotyledon leaf area. Four cotyledons ($n=4$, one cotyledon per plant) were used to calculate the total trichome number at 0, 1, 3, 5, 7, 9, 11, 13, and 15 d. Thus, a total of 72 plants were used.

RESULTS

To investigate the effects of continuous UV-B irradiation on pumpkin seedlings, we observed and analyzed their development for 15 d (Figs. 2–7). There were no clear differences between the adaxial surfaces of cotyledons of control plants and those of UV-B-irradiated plants at the start of the experiment (0 d) (Fig. 2). The adaxial surfaces of irradiated cotyledons were white and shiny after UV-B treatment for 3–15 d (Fig. 2a) compared with that of control plants. The adaxial surfaces of the control cotyledons were chlorotic at 15 d (Fig. 2b), presumably due to senescence, whereas those of irradiated cotyledons were not. In the control cotyledons, leaf area and epidermal cell area expanded gradually throughout the 15 d experiment (Fig. 3A, B). By contrast, expansion of leaf area and epidermal cell area was slightly reduced after UV-B irradiation for 3–15 d (Fig. 3A, B). In control cotyledons, total epidermal cell number was approximately 1.9–2.0 × 10$^6$ and did not change throughout the 15 d experiment (Fig. 3C). Similarly, the total epidermal cell number did not change significantly after UV-B irradiation for 15 d (Fig. 3C). The surface of control cotyledons at 0 d contained trichomes consisting of three cells (defined as normal trichomes) (Fig. 4A, three black arrowheads) with nuclear levels of 16.7–21.6 C (Figs. 4Ba, 5), which was greater than that in epidermal cells (1.8–2.4 C) (Figs. 4Bb, 5). The surface of the UV-B-irradiated cotyledons from 3 to 7 d contained smaller trichomes consisting of single cells (Fig. 6a), in addition to normal trichomes (Fig. 7). There were no clear differences between the adaxial surfaces of control cotyledons at 0 d and those of UV-B irradiated plants at the start of the experiment (0 d) (Fig. 2). The adaxial surfaces of irradiated cotyledons were white and shiny after UV-B treatment for 3–15 d (Fig. 2a) compared with that of control plants. The surface of control cotyledons at 0 d contained trichomes consisting of three cells (defined as normal trichomes) (Fig. 4A, three black arrowheads) with nuclear levels of 16.7–21.6 C (Figs. 4Ba, 5), which was greater than that in epidermal cells (1.8–2.4 C) (Figs. 4Bb, 5). The surface of the UV-B-irradiated cotyledons from 3 to 7 d contained smaller trichomes consisting of single cells (Fig. 6a), in addition to normal trichomes (Fig. 6a). Epidermal cells in cotyledons exposed to UV-B irradiation for 11–15 d were stained by toluidine blue O (Fig. 6c), whereas control cotyledons were not. Epidermal cells surrounding trichomes were expanded and stained by toluidine blue O at 11 and 15 d in both control and UV-B-irradiated plants (Fig. 6d). The total trichome number on the surface of the control cotyledons did not increase significantly throughout the 15 d experiment (Fig. 7). By contrast, the total trichome number increased remarkably after UV-B irradiation for 5–9 d, and stabilized after UV-B irradiation for 9–15 d (Fig. 7). The time point when smaller trichomes were observed coincided with the time point when total trichome number substantially increased on the surface of UV-B-irradiated pumpkin cotyledons. Thus, continuous UV-B irradiation of pumpkin seedlings for 15 d induces trichome formation through endoreduplication in tissues lacking active cell division (cotyledons).

The number of unfolded true leaves in control plants was zero at 0 d, one at 3 d, two at 7 d, three at 11 d, and four at 15 d (Fig. 2c–f). Similarly, the number of unfolded
true leaves in UV-B-irradiated plants was zero at 0 d, one at 3 d, two at 7 d, three at 11 d, and three at 15 d (Fig. 2c–e). Thus, continuous UV-B irradiation for 15 d slightly reduced the unfolding rate of true leaves in pumpkin seedlings. The expansion of true leaves was severely disrupted by UV-B irradiation for 15 d compared with that in controls (Fig. 2). In the control first leaves, leaf area and epidermal cell area expanded gradually throughout the 15 d experiment (Fig. 3D, E). By contrast, expansion of leaf area and epidermal cell area was reduced considerably after UV-B irradiation for 15 d (Fig. 3D, E). The slight reduction of leaf area and epidermal cell area in the first leaves after UV-B irradiation for 11–15 d (Fig. 3D, E) is due to UV-B-induced damage (Fig. 2). In the control first leaves, total epidermal cell number increased throughout the experiment for 11 d (Fig. 3F). The total epidermal cell number was reduced after UV-B irradiation for 15 d compared to that in the control (Fig. 3F). Thus, continuous UV-B irradiation of pumpkin seedlings for 15 d reduces cell division and expansion in tissues with active cell division (SAM including...
DISCUSSION

Trichomes are uni- or multi-cellular hairs that develop on the leaves, sepals, and stems of higher plants. It is clear that cell division does not occur during trichome formation in Arabidopsis because the trichomes consist of single cells (Melaragno et al., 1993; Hulskamp et al., 1994). In pumpkin and cucumber, most trichomes contain three cells (Fig. 4A, black arrowheads) (Yamasaki et al., 2007). The precise mechanism of trichome formation in pumpkin and cucumber, including whether cell division occurs, is unclear. Because trichome nuclear DNA levels are greater than those in epidermal cells in Arabidopsis, pumpkin, and cucumber, it is clear that trichome DNA undergoes endoreduplication during development. These results suggest that the increased trichome number results from endoreduplication of epidermal cells on the surface of pumpkin cotyledons.

Trichome number is influenced by plant hormones in higher plants. Jasmonic acid and gibberellin significantly stimulate trichome production in Arabidopsis leaves (Traw and Bergelson, 2003). Transient exposure to ethylene affects trichome number in cucumber hypocotyls (Kazama et al., 2004). Salicylic acid has a negative effect on trichome production in Arabidopsis (Traw and Bergelson, 2003). In the present study, continuous UV-B irradiation increased the total trichome number on the surface of pumpkin cotyledons (Fig. 7). It is possible that continuous UV-B irradiation affected the concentration of plant hormones such as ethylene, jasmonic acid, gibberellin, and salicylic acid, and they led to the increased total trichome number on the surface of pumpkin cotyledons.

Increased numbers of trichomes on the surface of pumpkin cotyledons is considered as a defense response against UV-B irradiation for the following reasons: (1) physical protection, (2) chemical protection, and (3) acquisition of UV-B tolerance by endoreduplication. Physical protection is reportedly caused by densely distributed trichomes that increase reflection of UV-B irradiation in two xeromorphic plants (olive and oak) and in Sonoran Desert plants (Ehleringer, 1984; Karabourniotis and Bergelson, 2003). Continuous UV-B irradiation for 15 d (Fig. 2). This tendency coincided well with the effects on SAM in cucumber seedlings (Yamasaki et al., 2014). Continuous long-term UV-B irradiation for 15–25 d in cucumber seedlings accelerated developmental stages such as true-leaf unfolding and male flower bud production (Yamasaki et al., 2014). Similar results might be obtained in pumpkin seedlings after continuous long-term UV-B irradiation for more than 15 d.

The effects of continuous UV-B irradiation on pumpkin and cucumber seedlings are summarized in Table 2. The method used for UV-B irradiation and the intensity of UV-B irradiation employed in the present study are essentially the same as those described in previous studies (Yamasaki et al., 2007; 2010; 2014); thus, the effects of UV-B irradiation on pumpkin and cucumber seedlings may be similar. However, it will be necessary to examine UV dose-dependent responses in both pumpkin and cucumber seedlings before any firm conclusions about this can be drawn. Continuous UV-B irradiation in pumpkin cotyledons does not induce rapid expansion of epidermal cells through active cell division (cotyledons) acquire defense responses against or tolerance to continuous UV-B irradiation in pumpkin seedlings.

Tissues undergoing active cell division (SAM including first leaves) in pumpkin seedlings were susceptible and damaged by continuous UV-B irradiation for 15 d (Fig. 2). The method used for UV-B irradiation and the intensity of UV-B irradiation employed in the present study are essentially the same as those described in previous studies (Yamasaki et al., 2007; 2010; 2014); thus, the effects of UV-B irradiation on pumpkin and cucumber seedlings may be similar. However, it will be necessary to examine UV dose-dependent responses in both pumpkin and cucumber seedlings before any firm conclusions about this can be drawn. Continuous UV-B irradiation in pumpkin cotyledons does not induce rapid expansion of epidermal cells through active cell division (cotyledons) acquire defense responses against or tolerance to continuous UV-B irradiation in pumpkin seedlings.

![Table 2](attachment:image)

<table>
<thead>
<tr>
<th>Cotyledon</th>
<th>Pumpkin</th>
<th>Cucumber</th>
</tr>
</thead>
<tbody>
<tr>
<td>Induction of whiteness and shininess</td>
<td>O</td>
<td>O'</td>
</tr>
<tr>
<td>Reduction of leaf area expansion</td>
<td>O</td>
<td>O'</td>
</tr>
<tr>
<td>Constant epidermal cell number</td>
<td>O</td>
<td>O'</td>
</tr>
<tr>
<td>Induction of rapid epidermal cell expansion surrounding trichomes (induction of endoreduplication)</td>
<td>×</td>
<td>O''</td>
</tr>
<tr>
<td>Increase of trichome number (induction of endoreduplication)</td>
<td>O</td>
<td>×''</td>
</tr>
<tr>
<td>First leaf</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduction of leaf area expansion</td>
<td>O</td>
<td>O'</td>
</tr>
<tr>
<td>Reduction of epidermal cell expansion</td>
<td>O</td>
<td>×''</td>
</tr>
<tr>
<td>Decrease of epidermal cell number (reduction of cell division)</td>
<td>O</td>
<td>O'</td>
</tr>
</tbody>
</table>

O = observed; × = not observed.

* Yamasaki et al., 2007; † Yamasaki et al., 2010; ‡ Yamasaki et al., 2014.
UVB EFFECTS ON PUMPKIN SEEDLINGS

surrounding trichomes, but increases trichome number (Table 2, Fig. 7). By contrast, continuous UV-B irradiation in cucumber seedlings does not increase trichome number but induces rapid expansion of epidermal cells surrounding trichomes (Table 2; Yamasaki et al., 2007, 2010). These results indicate that the induction of endoreduplication is common but the method of its expression differs in UV-B-irradiated pumpkin and cucumber cotyledons. Because the expansion of epidermal cells surrounding trichomes occurs on the surface of pumpkin cotyledons in control and UV-B-irradiated plants for 15 d (Fig. 6d), this phenomenon is not induced specifically by UV-B irradiation of pumpkin cotyledons. Reduced expansion of the leaf area of first leaves is due to the reduction of division and expansion of epidermal cells in the UV-B-irradiated pumpkin seedlings (Table 2, Fig. 3D–F), whereas it is due to reduced division of epidermal cells in the UV-B-irradiated cucumber seedlings. In the UV-B-irradiated cucumber seedlings, reduced epidermal cell division and expansion occurs in other true leaves but not in the first leaves (Yamasaki et al., 2014).

In summary, in both pumpkin and cucumber seedlings, continuous UV-B irradiation induces endoreduplication in tissues lacking active cell division (cotyledons), whereas this treatment reduces cell division in tissues with active cell division (SAM including first leaves). The former is classified as “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.” The sensitivity to UV-B irradiation, “defense response against UV-B irradiation,” whereas the latter is classified as “growth inhibition by UV-B irradiation.”

This work was partially supported by the Ministry of Education, Culture, Sports, Science and Technology, a Grant-in-Aid for Young Scientists (B) (no. 23780026 to S. Y.), the 5th Nissan Science Foundation, and the Saito Gratitude Foundation.

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