Turkish Journal of Biology

Volume 35 | Number 1 Article 8

1-1-2011

The effects of UV radiation on some structural and ultrastructural parameters in pepper (Capsicum longum A.DC.)

SIAVASH HOSSEINI SARGHEIN

JIRAIR CARAPETIAN

JALIL KHARA

Follow this and additional works at: https://journals.tubitak.gov.tr/biology

 Part of the Biology Commons

Recommended Citation

SARGHEIN, SIAVASH HOSSEINI; CARAPETIAN, JIRAIR; and KHARA, JALIL (2011) "The effects of UV radiation on some structural and ultrastructural parameters in pepper (Capsicum longum A.DC.)," *Turkish Journal of Biology*: Vol. 35: No. 1, Article 8. https://doi.org/10.3906/biy-0903-11
Available at: https://journals.tubitak.gov.tr/biology/vol35/iss1/8

This Article is brought to you for free and open access by TÜBİTAK Academic Journals. It has been accepted for inclusion in Turkish Journal of Biology by an authorized editor of TÜBİTAK Academic Journals. For more information, please contact academic.publications@tubitak.gov.tr.

Turk J Biol
35 (2011) 69-77
© TÜBİTAK
doi:10.3906/biy-0903-11

The effects of UV radiation on some structural and ultrastructural parameters in pepper (*Capsicum longum* A.DC.)

Siavash HOSSEINI SARGHEIN, Jirair CARAPETIAN, Jalil KHARA

Department of Biology, Faculty of Science, Urmia University, Urmia - IRAN

Received: 12.03.2009

Abstract: The objective of this study was to evaluate the effects on the structure and ultrastructure of pepper plants (*Capsicum longum* A.DC.) exposed to UV radiation under greenhouse conditions. The plants were grown in a growth chamber under uniform environmental conditions and after 35 days were exposed to UV-A and UV-C radiation for 15 and 8 days, respectively. Changes in root growth were not significant, but shoot growth decreased in UV-R-exposed plants and decreased significantly in UV-C-exposed plants. Leaf area also decreased in UV-R-exposed plants and decreased significantly in UV-C-exposed plants. Root thickness was not affected by UV treatment, but stem and leaf thickness significantly increased in response to UV-A and UV-C treatment. Stomata increased in number and size in UV-R-exposed plants. At the ultrastructural level, chloroplast thylakoids were dilated and starch reduction was observed. UV treatment resulted in the formation of crystals in the peroxisomes of mesophyll cells. The formation of these crystals was due to an increase in catalase activity, which is an antioxidant enzyme. The study shows that pepper plants were sensitive to UV and the findings provide insight into the physiological changes during UV exposure, and indicate this plant was more sensitive to UV-C radiation than to UV-A radiation.

Key words: UV radiation, *Capsicum longum* A.DC., structure, ultrastructure, chloroplast

Biberdeki (*Capsicum longum* A.DC.) bazı strüktürel ve ultrastrüktürel Parametreler üzerine UV-radyasyonunun etkileri

Özet: Bu çalışmanın amacı, seradaki UV radyasyonunun biber (*Capsicum longum* A.DC.) bitkilerinin strüktür ve ultrastrüktürü üzerine etkilerini değerlendirmektir. Bu bitkiler, büyüme odalarında standart bir çevrede yetiştirilmiştir ve 35 gün sonra sırasıyla 15 ve 8 gün UV-A ve UV-C'ye maruz bırakılmıştır. Bu çalışmada, kök büyümesinde değişikliklerin önemli olmadığı bulunmuştur, fakat UV-R'ye maruz kalmış bitkilerde filizin büyümesi azalmış ve bu azalma UV-C muamelesinde kayda değerdir. UV-R'ye maruz bırakılmış bitkilerde yaprak alanı da küçülmüştür ve bu küçülme UV-C muamelesinde önemlidir. Kök kalınlığı, UV uygulamasında etkilenmemiştir, fakat yaprak ve gövde kalınlığı hem UV-A hem de UV-C muamelelerinde önemli bir şekilde artmıştır. UV-R'ye maruz bırakılmış bitkilerde stomanın sayısı ve büyüklüğü de artmıştır. Ultrastrüktür seviyede, kloroplast tilakoidlerinin şiştiği ve nişastanın azaldığı gözlenmiştir. UV muamelesi, mezofil hücrelerin peroksizomlarındaki kristalize kalıntının oluşması ile sonuçlanmıştır. Bu kristallerin oluşumu antioksidan bir enzim olan katalazın aktivitesinin artmasından dolayıdır. Bu çalışma, biber bitkilerinin UV'ye duyarlı olduğunu göstermiş ve bu bulgular, UV'ye maruz kalma esnasında fizyolojik değişikliklerin anlaşılmasını sağlamıştır ve bu bitkilerin UV-A radyasyonundan daha çok UV-C'ye duyarlı olduğunu göstermiştir.

Anahtar sözcükler: UV, radyasyon, *Capsicum longum* A.DC., strüktür, ultrastrüktür, kloroplast

Introduction

UV radiation is the part of the non-ionizing region of the electromagnetic spectrum that comprises approximately 8%-9% of total solar radiation (1,2). UV is traditionally divided into 3 wavelengths. UV-C (200-280 nm) is extremely harmful to living organisms, but not relevant under natural conditions of solar irradiation. UV-B (280-320 nm) is of particular interest because although this wavelength represents only approximately 1.5% of the total spectrum, it can have a variety of damaging effects in plants. UV-A (320-400 nm) represents approximately 6.3% of the incoming solar radiation and is the least hazardous part of UV radiation (3). Projections indicate that solar UV-B radiation will reach peak levels on the Earth's surface within the next few years (4). However, it is expected that UV-B radiation could fall to pre-ozone depletion levels by 2050 if the Montreal Protocol is fully implemented by all member countries (5). Measurable attenuation of the stratospheric ozone layer and the consequent increase in terrestrial UV-B radiation has increased 6%-14% since the 1970s (6).

Increased UV exposure has been shown to alter the biotic relationships of higher plants, as demonstrated by the changes in plant disease susceptibility and the balance of competition between plant species (7). The influence of UV radiation on growth appears to be mediated by phytohormones, either via photodestruction or enzymatic reactions. Overall, the effects of UV radiation vary, both among species and among cultivars of a given species. Of those plants that have been tested, a large proportion exhibited reduced plant growth (plant height, dry weight, leaf area, etc.), photosynthetic activity, and flowering (7). Stem and leaf thickness are altered in UV-treated plants. At the ultrastructural level it has been observed that changes occur in chloroplasts and peroxisomes in response to UV radiation (8).

UV radiation above ambient levels may inhibit plant growth, development, reproduction, and photosynthesis (9-11); however, plant sensitivity to UV radiation differs between species (12) and varieties (13-15). It is modified by the plant growth rate (16), developmental stage (17), growth form (herbs cf. trees), and functional type (18). Additionally, air temperature (19), atmospheric carbon dioxide concentrations (20), and soil nitrogen (21,22), phosphorus (23), and moisture (24) content may affect plant sensitivity to UV radiation (25).

The aim of the present study was to examine a variety of parameters considered to play an important role in plant protection against UV radiation, and to obtain an overview of the way that important crop plants fare when exposed to elevated levels of UV radiation. We analyzed changes in root, stem, and leaf thickness, and the length and number of stomata were also measured. Additionally, ultrastructural level changes in chloroplasts and peroxisomes were examined.

Materials and methods

Plant material

Red pepper (*Capsicum longum* A.DC.), commonly called chili, is a member of the family *Solanaceae*. Chili seeds (obtained from Artan Co., Iran) were sterilized with 10% sodium hypochlorite for 10 min and were then soaked in distilled water. Germination occurred at a rate of about 90%. The soil used in pots was obtained from a field and mixed with sand (1:5 v/v). The mixture was autoclaved at 121 °C for 4 h before use.

The germinated seeds were grown in 45 pots measuring 20 cm in diameter in a greenhouse. After 35 days of growth under uniform conditions they were divided into 3 sets of 15 pots. One set served as the control, another set received UV-C radiation for 8 days, which was produced by a UV-C germicidal lamp (TUV/G30T8, Philips, Holland) that provided an irradiation dose of approximately 17.2 kJ m^{-2} d^{-1}, and the third set was exposed to UV-A radiation for 15 days, which was produced by 2 insecticide UV-A lamps (F20T9/BL, Hitachi, Japan) that produced an irradiation dose of approximately 18.9 kJ m^{-2} d^{-1}.

Plants were grown at 35/26 °C (day/night) 14 h of light and 10 h of dark, and were alternately watered with half-strength Hoagland solution and distilled water. Plant height and root length were measured. Leaf area was calculated using Flächenberechnung-einer-sw-Grafik software (A. Kraf Software, 1995).

Light microscopy

Leaf, root, and stem thickness were measured using a photomicroscope fitted with a micrometer,

employing transverse sections cut from material obtained from the 3 different treatments. The length and number of stomata were also measured.

Electron microscopy

After UV exposure leaf samples were fixed in glutaraldehyde (3%), and then osmium tetroxide (1%) using phosphate buffer and were routinely embedded in Epon. Leaf samples were collected from 3 different plants and 5 blocks made from each. To assure random pictures were obtained, 3 blocks were chosen and from each several ultra-thin sections were cut and mounted in grids with 100-square mesh. Photographs of mesophyll cells were made using a Philips CM 100 BioTWIN electron microscope.

Statistical analysis

Values presented in the text indicate mean values ± S.E.M. of each treatment. The significance of differences between the control, and UV-C- and UV-A-exposed material was analyzed using Tukey's MRT; $P < 0.05$ was considered statistically significant (26).

Results and discussion

Root and shoot length

In comparison with the control plants, root length was not significantly changed by UV exposure, but shoot length decreased and this reduction in UV-C-exposed plants was greater than in UV-A-exposed plants (Figure 1). The growth of many species is reduced in response to UV treatment. Similar changes have been observed in sunflower and corn seedlings (27), *Impatiens capensis* (28), *Gossypium hirsutum* (4), *Pisum sativum* (29), and *Fagopyrum tataricum* (30). This reduction is associated with UV-dependent destruction of the growth regulator indole-3-acetic acid (IAA) and formation of growth-inhibiting IAA photoproducts. Inhibition of elongation in UV-irradiated plants might also be due to the action of peroxidases working as IAA-oxidase, causing a decrease in cell wall extensibility (31).

Leaf area

UV exposure decreased leaf area and this decrease was significant in the UV-C-exposed plants (Figure 2). Similar changes were reported in sunflower and corn (27), cotton (4), pea (29), *Impatiens capensis* (28),

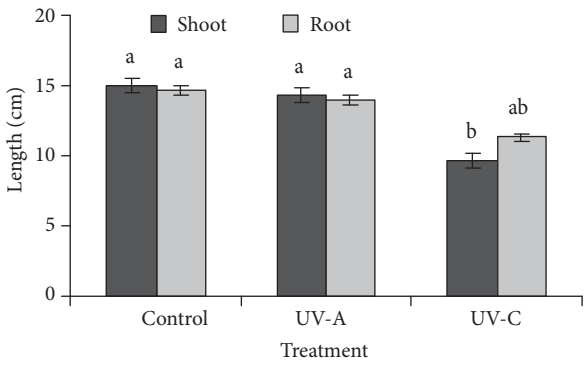

Figure 1. The length of root and shoot of plants exposed to UV radiation (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05

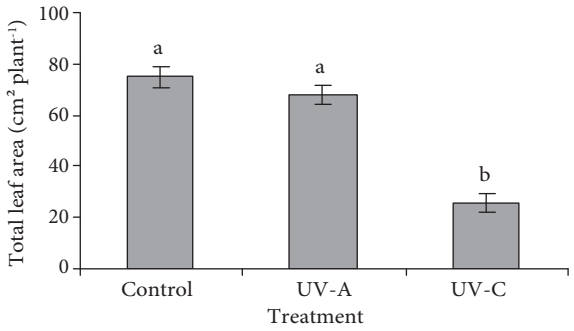

Figure 2. Total leaf area of plants exposed to UV radiation (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05

Solanum tuberosum (8), and ***Fagopyrum*** *tataricum* (30). Reduced leaf area under UV radiation is a photomorphogenic response that can limit the damage to leaf tissues caused by UV radiation (11). The decrease in leaf area in response to UV radiation was the result of changes in both the rate and extent of cell division and elongation. UV radiation decreased the proportion of mitotically active cells and increased the time taken for cell division (32).

Root and stem thickness

In comparison with the control plants, root thickness was not significantly changed by UV exposure, as observed by light microscopy of cross sections (Figures 3 and 4). As compared with the control treatment, UV exposure significantly increased stem thickness, which was greater in UV-C-exposed plants than in UV-A-exposed plants

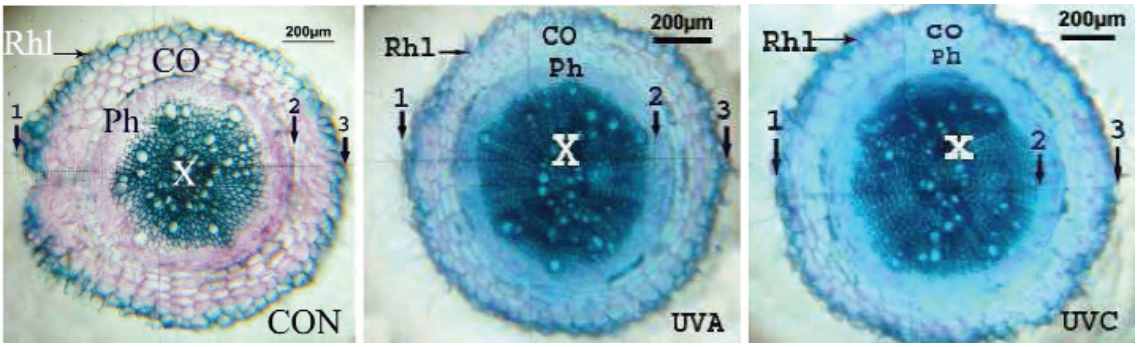

Figure 3. Root thickness of plants exposed to UV radiation as compared with the control.co, cortex; Ph, phloem; X, xylem; Rhl, root hair layer.

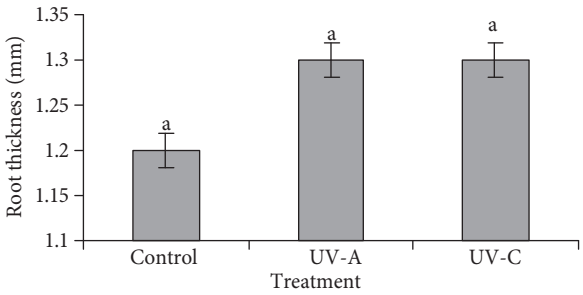

Figure 4. The effects of UV radiation on root thickness (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05

(Figures 5 and 6). It was reported that UV radiation increases ethylene production and that this hormone decreases stem elongation and increases stem thickness (33). In contrast, UV exposure decreased stem thickness in *Fagopyrum tataricum* (30).

Leaf thickness

In comparison with the control treatment, UV exposure significantly increased leaf thickness. This increase was greater in UV-C-exposed plants than in UV-A-exposed plants (Figures 7 and 8). Increased leaf thickness was reported in *Brassica campestris* (34), potato (8), soybean (35), and *Brassica napus* (36). Increased leaf thickness is considered a protective mechanism against damage caused by UV radiation (3). Contrary to these reports, leaf thickness in *Zea mays* decreased (37). In Scots pine thickening of epidermal and hypodermal cell layers has been observed in response to UV treatment (38).

Stomatal length and density

The effects of UV on the length and density of stomata cells was also examined. In comparison with the control treatment, UV exposure significantly increased the length of guard cells. This increase was

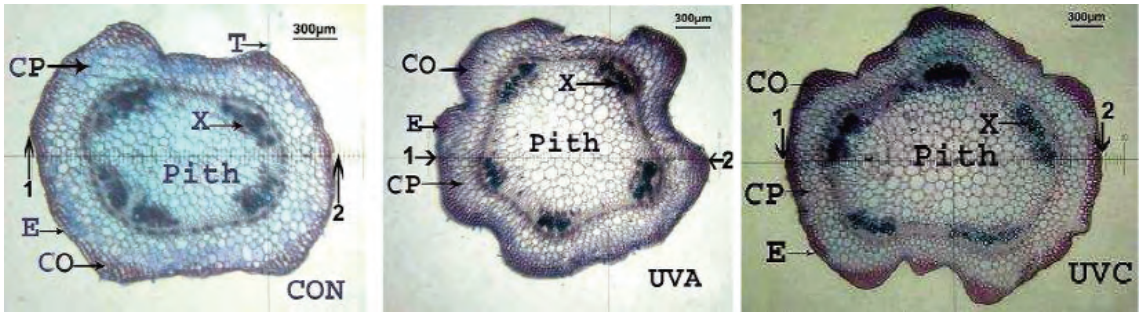

Figure 5. Stem thickness of plants exposed to UV radiation as compared with the control. cp, cortex; X, xylem; co, collenchyma; E, epidermis; T, trichom.

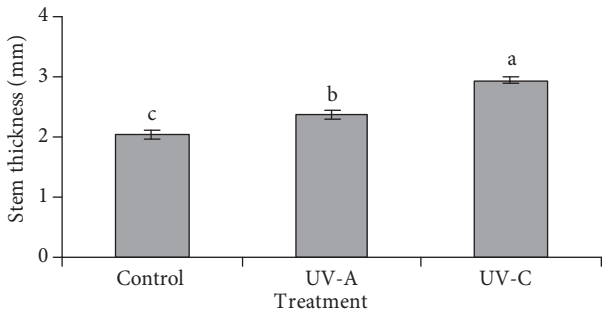

Figure 6. The effects of UV radiation on stem thickness (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05

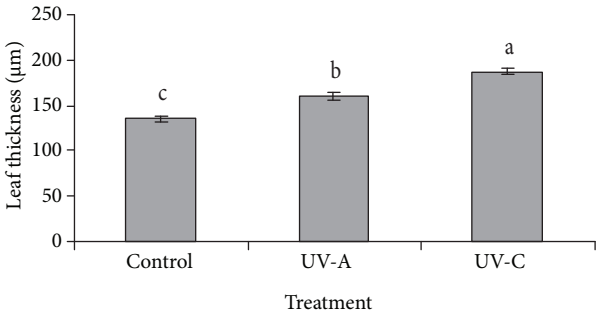

Figure 8. The effects of UV radiation on leaf thickness (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05.

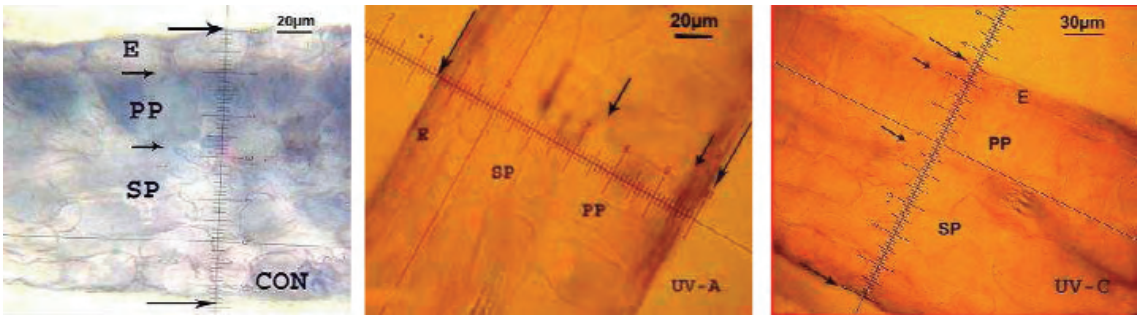

Figure 7. Leaf thickness of plants exposed to UV radiation as compared with the control. pp, palisade parenchyma; sp, spongy parenchyma; E, epidermis.

greater in UV-C-exposed plants than in UV-A-exposed plants (Figures 9 and 10). UV radiation also caused an increase in the frequency of stomata in epidermal cells, as compared with the control; this increase was significant in UV-C-exposed plants (Figures 11 and 12). Similar changes have been reported in cotton (4), acacias, and eucalyptus (39).

Ultrastructural study

The most notable effects caused by UV radiation are illustrated in Figure 13, which shows part of a

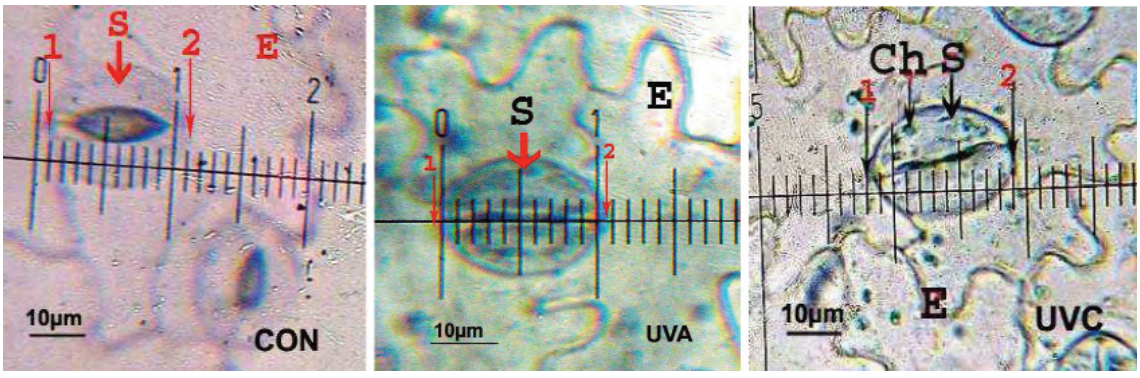

Figure 9. Stomata length of plants exposed to UV radiation as compared with the control. S, stoma; ch, chloroplast; E, epidermis.

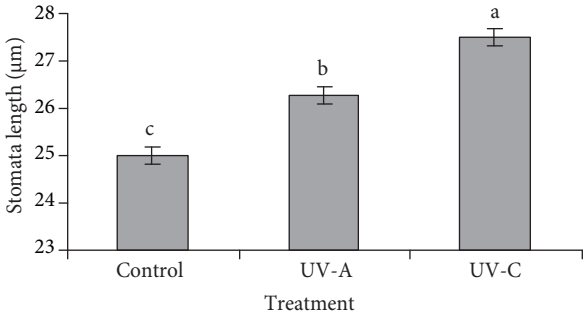

Figure 10. The effects of UV radiation on stomata length (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05

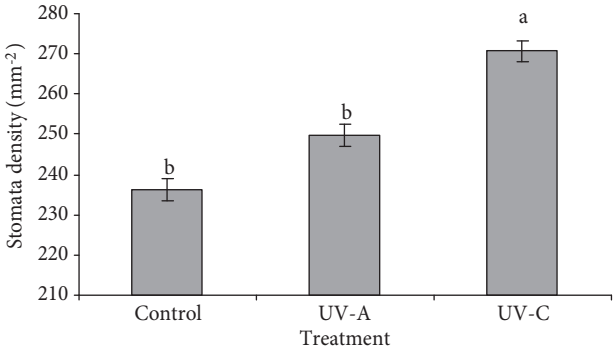

Figure 12. The effects of UV radiation on stomata density (mean ± SE) as compared with the control. Means followed by the same letters are not significantly different; Tukey-Kramer-HSD at P = 0.05.

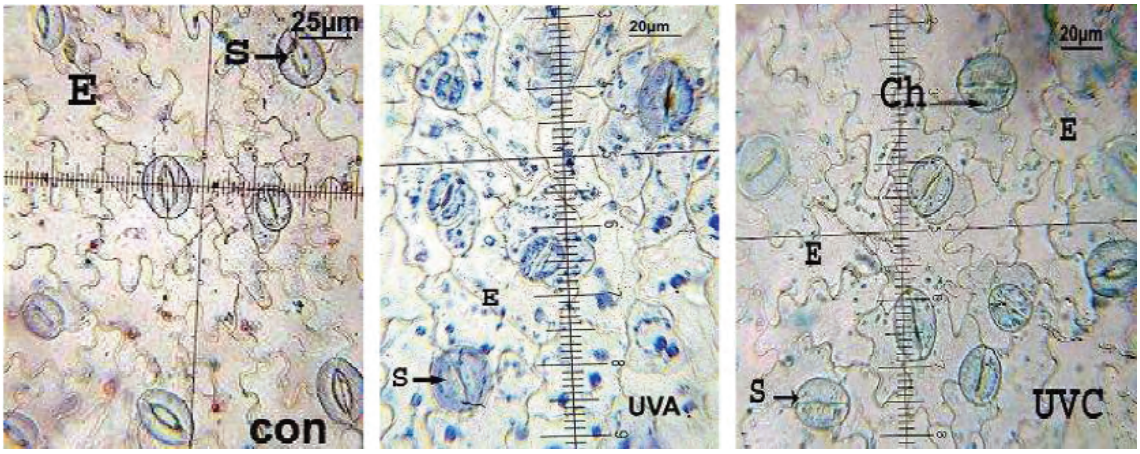

Figure 11. Stomata density of plants exposed to UV radiation as compared with the control. S, stoma; ch, chloroplast; E, epidermis.

mesophyll cell. In comparison with the control, UV-exposed cells contained chloroplasts that had begun to lose their structural integrity. The orderly pattern of grana and stroma thylakoids was lost, and some of the thylakoids appeared slightly dilated.

Among the various organelles, the chloroplasts appear to be the most sensitive to UV radiation (3). UV radiation may cause more serious ultrastructural alterations, as was observed in other plant species. In a study of *Pisum sativum*, UV-B induced ultrastructural changes, including dilation of the nuclear membrane, chloroplast swelling, thylakoid dilation, rupture of chloroplast outer membranes, swollen cisternae in the endoplasmic reticulum, and vesiculation of the plasmalemma and tonoplast (40). Thylakoid dilation in response to UV radiation has also been reported in red algae *Palmaria decipiens* (41), whereas in potato thylakoids were unaffected (8).

Another effect of UV radiation is shown in Figure 14. It was observed that UV-exposed cells had chloroplasts that contained fewer starch grains than did control cells. Starch grains are synthesized during photosynthesis (42); therefore, all changes in the structure and function of the chloroplast results in a reduction in starch. A reduction in starch in response to UV radiation was also reported in potato (8). In contrast, pea cv. *Greenfas* plants that were exposed to supplementary UV radiation were observed to

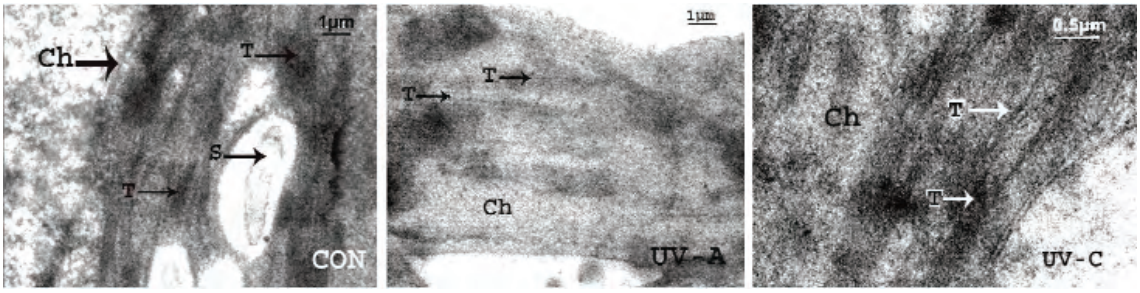

Figure 13. The effects of UV radiation on thylakoids as compared with the control. Ch, chloroplast; T, thylakoid; S, starch.

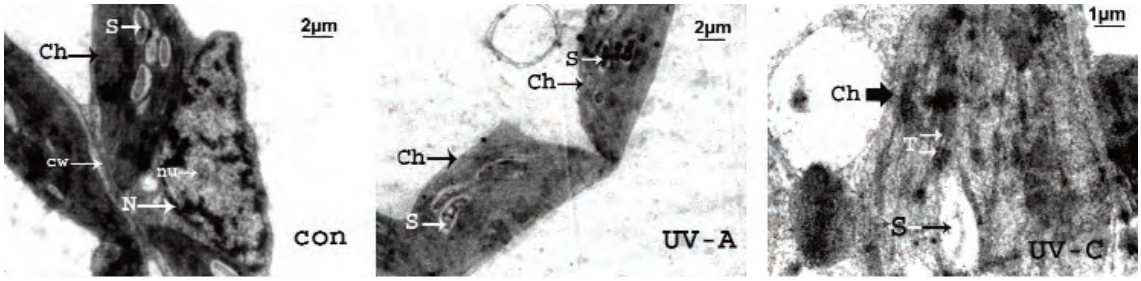

Figure 14. The effects of UV radiation on starch grain as compared with the control. Ch, chloroplast; T, thylakoid; S, starch; cw, cell wall; N, nucleus; nu, nucleolus.

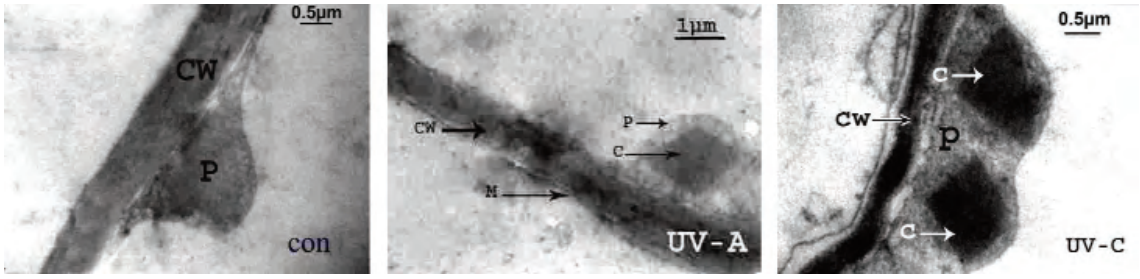

Figure 15. The effects of UV radiation on peroxisomal crystalline as compared with the control. M, cytoplasmic membrane; CW, cell wall; C, crystalline; P, peroxisomes.

accumulate more starch grains. This higher concentration of starch, as compared to the control, was due to immobilization rather than any increase in starch synthesis, because UV radiation inhibits the synthesis of amylolytic enzymes (43). Accumulation of starch grains has also been observed in corn, due to mitochondrial damage resulting from UV treatment; therefore, starch grains stop functioning as a respiration substrate and accumulate in chloroplasts (37).

Another important ultrastructural observation was changes in the peroxisomes in UV-exposed plants. Catalase enzymes are located in these organelles. Catalase is a constitutive component of peroxisomes, and detoxifies H_2O_2 into water and oxygen, and decreases its damage to cells (44). Thus, its activity usually increases under oxidative stress. UV radiation also induces oxidative stress and catalase is one of the key enzymes of the antioxidant

defense system (8). In the present study UV radiation induced the formation of crystals in peroxisomes (Figure 15). The crystals in the peroxisomes of UV-exposed plants were made of active catalase. Similar changes have been reported in UV-exposed potato leaves. It was observed that the increase in catalase activity caused by UV exposure occurred simultaneously with the appearance of crystals in the peroxisomes of potato plants (8). Another study reported that these crystals, which were made by an accumulation of a catalase isoform, are different from the catalase in the peroxisomal matrix of sunflower cotyledon peroxisomes (45).

Acknowledgments

The authors thank Dr. Farshid and Mr. Kahroba for their help at the Electron Microscopy Center of Urmia University.

Corresponding author:

Siavash Hosseini SARGHEIN

Department of Biology,

Faculty of Science,

Urmia University, Urmia - IRAN

E-mail: sihosseini@yahoo.com

References

1. Coohill TP. Ultraviolet action spectra (280 nm to 380 nm) and solar effectiveness spectra for higher plants. Photochem Photobiol 50: 451-457, 1989.
2. Frederick JE. Ultraviolet sunlight reaching the Earth's surface. A review of recent research. Photochem Photobiol 57: 175-178, 1993.
3. Hollosy F. Effects of ultraviolet radiation on plant cells. Micron 33: 179-197, 2002.
4. Kakani VG, Reddy KR, Zhao D et al. Effects of ultraviolet-B radiation on cotton (*Gossypium hirsutum* L.) morphology and anatomy. Ann Bot 91: 817-826, 2003.
5. Van der Leun JC, Tang X, Tevini M. Environmental effects of ozone depletion: 1998 assessment. J Photochem Photobiol 46: 5-19, 1998.
6. UNEP/WMO. Executive summary, Scientific assessment of ozone depletion: 2002. Prepared by the Scientific Assessment Panel of the Montreal Protocol on Substances that Deplete Ozone Layer. Released by WMO/UNEP on 23 Aug. 2002.
7. Teramura AH, Tevini M, Bornman JF et al. Terrestrial plants. Environmental effects of ozone depletion. Nairobi: United Nations environment programme; Chapter 3, 1991.
8. Santos I, Fidalgo F, Almeida JA et al. Biochemical and ultrastructural changes in leaves of potato plants grown under supplementary UV-B radiation. Plant Sci 167: 925-935, 2004.
9. Teramura AH, Sullivan JH. Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. Photosynth Res 39: 463-473, 1994.
10. Rozema J, Van de Staaij J, Bjorn LO et al. UV-B as an environmental factor in plant life: stress and regulation. Trends Ecol Evol 12: 22-28, 1997.
11. Jansen MAK, Gaba V, Greenberg BM. Higher plants and UV-B radiation: balancing damage, repair and acclimation. Trends Plant Sci 3: 131-135, 1998.
12. Teramura AH. Effects of ultraviolet-B radiation on the growth and yield of crop plants. Physiol Plantarum 58: 415-427, 1983.
13. Reed HE, Teramura AH, Kenworthy WJ. Ancestral U.S. Soybean cultivars characterized for tolerance to ultraviolet-B radiation. Crop Sci 32: 1214-1219, 1992.
14. Barnes PW, Maggard S, Holman SR et al. Intraspecific variation in sensitivity to UV-B radiation in rice. Crop Sci 33: 1041-1046, 1993.
15. Correia CM, Areal ELV, Torres-Pereira MS et al. Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. I. Growth and morphological aspects. Field Crop Res 59: 81-89, 1998.
16. Eichhorn M, Dohler G, Austen H. Impact of UV-B radiation on photosynthetic electron transport of *Wolffia arrhiza* L. Wimm. Photosynthetica 39: 613-618, 1993.
17. Teramura AH, Sullivan JH. Soybean growth responses to enhanced levels of ultraviolet-B radiation under greenhouse conditions. Am J Bot 74: 975-979, 1987.
18. Gwynn-Jones D, Lee J, Johanson U et al. The responses of plant functional types to enhanced UV-B radiation. In: Rozema J, ed. Stratospheric ozone depletion: the effects of enhanced UV-B radiation on terrestrial ecosystems. Leiden, The Netherlands: Backhuys Publishers, 1999: pp.173-185.
19. Mark U, Tevini M. Effects of solar ultraviolet-B radiation, temperature and CO_2 on growth and physiology of sunflower and maize seedlings. Plant Ecol 128: 224-234, 1997.
20. Sullivan JH. Effects of Increasing UV-B Radiation and Atmospheric CO_2 on Photosynthesis and Growth: Implications for Terrestrial Ecosystems. Plant Ecol 128: 194-206, 1997.
21. Hunt JE, McNeil DL. Nitrogen status affects UV-B sensitivity of cucumber. Aust J Plant Physiol 25: 79-86, 1998.
22. Correia CM, Coutinho JF, Bjorn LO et al. Ultraviolet-B radiation and nitrogen effects on growth and yield of maize under Mediterranean field conditions. Eur J Agron 12: 117-125, 2000.

23. Murali NS, Teramura AH. Effects of UV-B irradiance on soybean. VI. Influence of phosphorus nutrition on growth and flavonoid content. Physiol Plantarum 63: 413-416, 1985.

24. Sullivan JH, Teramura AH. Field study of the interaction between solar ultraviolet-B radiation and drought on photosynthesis and growth in soybean. Plant Physiol 92: 141-146, 1990.

25. Musil CF, Chimphango SBM, Dakora FD. Effects of ultraviolet-B radiation on native and cultivated plants of Southern Africa. Ann Bot 90: 127-137, 2002.

26. SAS. The SAS System Version 7 for Windows. SAS Institute, Cary. 2000.

27. Tevini M, Mark U, Saile-Mark M. Effects of enhanced solar UV-B radiation on growth and function of crop plant seedlings. Curr Top Plant Biochem Physiol 10: 13-31, 1991.

28. Dixon P, Weinig C, Schmitt J. Susceptibility to UV damage in *Impatiens capensis* (Balsaminaceae): testing for opportunity costs to shade-avoidance and population differentiation. Am J Bot 88: 1401-1408, 2001.

29. Nogués S, Allen DJ, Morison JIL et al. Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. Plant Physiol 117: 173-181, 1998.

30. Yao Y, Xuana Z, Li Y et al. Effects of ultraviolet-B radiation on crop growth, development,yield and leaf pigment concentration of tartary buckwheat (*Fagopyrum tataricum*) under field conditions. Eur J Agron 25: 215-222, 2006.

31. Ros J. On the effect of UV-radiation on elongation growth of sunflower seedlings (*Helianthus annuus* L.) (Thesis), PhD, in Karlsr. Beitr. Entw. Okophysiol. 8, Tevini, M. (ed.), Bot. Inst. II, Karlsruhe. 1990.

32. Hopkins L, Bond MA , Tobin AK. Ultraviolet-B radiation reduces the rates of cell division and elongation in the primary leaf of wheat (*Triticum aestivum* L. cv Maris Huntsman). Plant Cell Environ 25: 617-624, 2002.

33. Ros J, Tevini M. Interaction of UV radiation and IAA during growth of seedlings and hypocotyl segments of sunflower. J Plant Physiol 146: 295-302, 1995.

34. Bornman JF, Vogelmann TC. Effect of UV-B radiation on leaf optical properties measured with fibre optics. J Exp Bot 42: 547-554, 1991.

35. Murali NS, Teramura AH, Randall SK. Response differences between two soybean cultivars with contrasting UV-B radiation sensitivities. Photochem Photobiol 48: 653-657, 1988.

36. Cen YP, Bornman JF. The effect of exposure to enhanced UV-B radiation on the penetration of monochromatic and polychromatic UV-B radiation in leaves of *Brassica napus*. Physiol Plantarum 87: 249-255, 1993.

37. Santos I, Almeida J, Salema R. Plants of *Zea mays* L. developed under enhanced UV-B radiation. I. Some ultrastructural and biochemical aspects. J Plant Physiol 141: 450-456, 1993.

38. Turunen M, Sutinen ML, Derome K et al. Ecophysiological responses of subarctic scots pine to ultraviolet (UV) radiation. Pol Bot Studies 19: 143-150, 2005.

39. Liu LX, Shou-Min X, Woo KC. Solar UV-B radiation on growth, photosynthesis and the xanthophyll cycle in tropical acacias and eucalyptus. Environ Exp Bot 54: 121-130, 2005.

40. Brandle JR, Campbell WF, Sisson WB et al. Net photosynthesis, electron transport capacity, and ultrastructure of *Pisum sativum* L.exposed to ultraviolet-B radiation. Plant Physiol 60: 165-169, 1977.

41. Holzinger A, Lutz C. Algae and UV irradiation: Effects on ultrastructure and related metabolic functions. Micron 37: 190-207, 2006.

42. Fahn A. Plant Anatomy. 4th ed. Pergamon Press. Oxford; 1990: pp. 21.

43. Kovacs E, Keresztes A. Effect of gamma and UV-B/C on plant cells. Micron 33: 199-210, 2002.

44. Zancan S, Suglia I, La Rocca N et al. Effects of UV-B radiation on antioxidant parameters of iron-deficient barley plants. Environ Exp Bot 63: 71-79, 2008.

45. Kleff S, Sander S, Mielke G et al. The predominant protein in peroxisomal cores of sunflower cotyledons is a catalase that differs in primary structure from the catalase in the peroxisomal matrix. Eur J Biochem 245: 402-410, 1997.