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Leaf Development of Rurnex patientia L. Exposed to UV Irradiation (280-320 nm)

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LEAF DEVELOPMENT OF *RUMEX PATIENTIA* L. EXPOSED TO UV IRRADIATION (280-320 nm)

by

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Judith G. Dickson

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ABSTRACT

Leaf Development of Rumex patientia L.

Exposed to UV Irradiation (280-320 nm)

by

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Utah State University, 1978

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Two factors which affect leaf ontogeny and ultimate leaf size: (1) the rate and duration of cell expansion, and (2) the rate and duration of cell division, were examined for their role in the slowed early growth rate and smaller ultimate leaf size when plants are exposed to ultraviolet-B (UV-B) radiation. Rumex patientia L. was grown in controlled environment chambers under enhanced UV-B radiation (equivalent to daily solar UV-B irradiation at 40^{o} N latitude in mid-May with an atmospheric ozone concentration of 0.20 atm-cm) and control treatments. The pattern of growth as expressed in changes of mean cell size of two distinct cell types, tissue cell density, and length of the entire blade are consistent with the hypothesis that the radiation primarily affects cell division rather than cell expansion. Furthermore, it appears that the radiation probably alters the rate rather than the duration of cell division. An understanding of the mechanism of radiation damage should facilitate prediction of how this stress may interact with other stresses to which plants are normally subjected.

(27 pages)

INTRODUCTION

The effect of pollutants on the stability of the stratospheric ozone layer has been of recent concern (Hammond, 1975). In the event of a partial reduction in the thickness of the ozone column by catalytic depletion (Cicerone et al., 1974; Grobecker et al., 1974; Johnston, 1971; Molina and Rowland, 1974), there would be a predictable increase in the quantity of ultraviolet-B radiation (UV-B, 280-320 nm) reaching the Earth (Bener, 1972; Green et al., 1974). In higher plants it has been shown that UV-B radiation of the nature one would expect from such an ozone reduction, could potentially depress photosynthetic rates (Sisson and Caldwell, 1976; Van and Garrard, 1976). It has also been reported that the rate of early leaf growth can be effectively reduced below a level solely attributable to photosynthate limitation (Sisson and Caldwell, 1976). The focus of the following research was to investigate the mechanism by which UV-B radiation results in the slowed rate of early leaf growth and ultimately smaller leaves.

Leaf ontogeny and ultimate leaf size are determined by three factors: (1) the rate and duration of cell expansion, (2) the rate and duration of cell division, and (3) the number of cells in the leaf primordium. Of these processes, the first two were examined for their role in the reduction of leaf growth by UV-B radiation. The number of cells in a leaf primordium was eliminated from concern by experimental design. Thus, the following hypotheses were introduced:

1) Cell division proceeds normally in both treatments, but the rate or duration of cell expansion is reduced by UV-B radiation.

2) Cell expansion proceeds normally in both treatments, but the rate or duration of cell division is depressed by UV-B radiation.

In this paper data are presented describing the altered pattern of cell division and cell expansion in leaves exposed to an enhanced UV-B radiation. Preliminary evidence supports the hypothesis that inhibition of cell division as opposed to reduced cell expansion is the primary mechanism resulting in smaller leaves and slower early growth rates of leaves subjected to UV-B radiation.

METHODS

Seedlings of Rumex patientia L. were planted into 10x10-cm pots and placed in a growth chamber where pretreatment conditions were identical to those under which the experiment would be conducted apart from the UV-B radiation supplement. Based on the uniformity of growth prior to the initiation of the fifth leaf, 24 plants were chosen and paired for this experiment. One of each pair was randomly selected for the control or UV-B treatments. Pairs were maintained identically with respect to pot position in the chamber and the orientation and angle of the fifth leaf in order to reduce the variation in growth due to small differences in chamber microclimate.

Growth chambers

The controlled environment chambers were equipped with a 6000-W Osram Co. xenon arc burner, the visible irradiation from which was maintained at 750 μeinsteins$\cdot m^{-2} \cdot s^{-1}$ (400-700 nm) as measured by a Lambda Co. Model LI-190-SR quantum sensor. The xenon arc was in quartz envelopes which in turn were enclosed in 2-mm Schott Co. WG-320 glass

filters which effectively absorbed radiation of wavelengths less than 300 nm. In addition, three Westinghouse FS-40 "sunlamps" were set parallel in a frame oriented lengthwise in the chamber. The frame was suspended 27 cm above the pots which were set in two rows corresponding to the intervals between the three lamps. Supplemental UV-B radiation was supplied by "sunlamps" filtered with Kodacel TA-401 (10 mil) plastic film which was replaced daily to maintain the desired radiation environment. The control regime included lamps filtered by Mylar Type 'A' (10 mil) plastic film. A general description of this lamp-filter system was reported by Sisson and Caldwell (1975).

The spectral irradiance from these lamp systems is shown in Figure 1. Due to the greater visible and UV-A (320-400 nm) irradiance in the natural environment, a comparison of spectra from growth chambers and those predicted for global irradiance at various atmospheric ozone concentrations is difficult. The growth chamber and predicted natural irradiation can, however, be related in terms of the biologically effective UV-B irradiance, $UV\text{-}B_{BE}$, which is calculated by weighting the spectral irradiance with a generalized plant action spectrum (Caldwell, 1971; Sisson and Caldwell, 1977). The integral thus obtained for $UV\text{-}B_{BE}$ during mid-May ($40^{o}N$ latitude and an ozone concentration of 0.34 atm-cm) is approximately 1000 $J \cdot m^{-2} \cdot day^{-1}$, using the model of Green et al. (1974) for solar spectral irradiance. In the growth chambers, the $UV\text{-}B_{BE}$ dose was calculated to be 2200 $J \cdot m^{-2} \cdot day^{-1}$ and 100 $J \cdot m^{-2} \cdot day^{-1}$, for enhanced UV-B and control treatments, respectively. This UV-B treatment corresponds approximately to a 40% decrease in ozone concentration (0.20 atm-cm) under these conditions (Green et al., 1974).

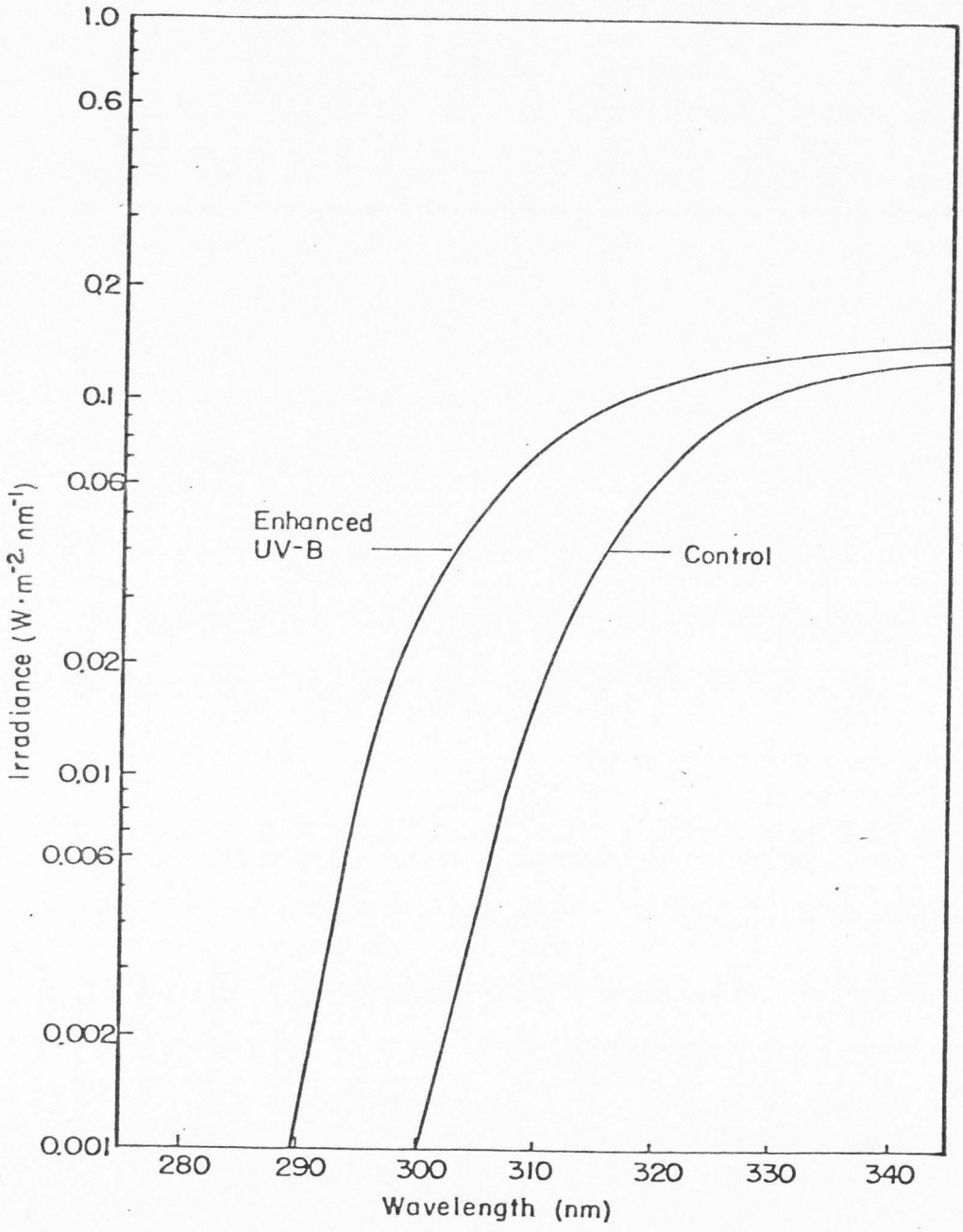

Figure 1. Spectroradiometer measurements of spectral irradiance in controlled environment chambers. Irradiation was supplied by a 5000-W xenon arc lamp with Schott Co. WG-320 glass filters and Westinghouse Co. FS-40 lamps filtered with Mylar Type 'A' (10 mil) plastic film (CONTROL treatment) and Kodacel TA 401 (10 mil) plastic film (UV-B ENHANCED treatment).

The simulated day in the growth chambers was 11 hours with the FS-40 lamps on during the middle 7 hours. The temperature and humidity cycles represented a mid-May condition at which time Rumex patientia begins growth in the field. The daily maximum was 28 C, 20% RH and minimum was 13 C, 40% RH.

Leaf measurements

The length of the fifth leaf was recorded daily before the "sunlamps" came on. At this time and at mid-day, pots were rotated 90° and advanced one position in the clockwise direction to minimize effects of small irregularities in the radiation field. On the second day of the experiment, the fifth leaf was sufficiently long to be tied back with white string in order to expose the abaxial surface to the overhead source of UV radiation. This angle of inclination was similar for each pair of plants. As the leaf grew, it was gently trained to a horizontal position.

On the 3rd, 4th, 6th and 16th days, three pairs of plants were chosen at random and the fifth leaf was sampled. Recording was made of total leaf weight, and weight of the blade and petiole separately. The leaf was then bisected longitudinally. One half was sectioned and fixed in formal acetic acid for tissue preservation. This tissue was later dehydrated in a tertiary-butyl alcohol series, embedded in paraffin, sectioned at 10 µm or 20 µm, and stained with toluidine blue-O (Sass, 1958). The slides thus obtained were used for cell size determination. Fifty measurements were made near the midrib on the horizontal (parallel to the plane of the blade) and vertical dimensions of both the upper epidermis and the upper palisade mesophyll. The cell types

were chosen because of their characteristic shape, resulting from expansion in perpendicular planes, and their developmental relation as adjacent tissues.

The other half of the leaf was weighed, cut into thirds by length, and reweighed. The area of each section was determined from tracings with a Lambda Model LI-3000 portable area meter. For eventual volume calculations, the thickness of each section was determined with a micrometer (Zeus Co.). Thickness of sections that were too small for measurement was estimated based on a correlation between thickness as measured on fixed and fresh tissue.

These pieces were then placed in 2-3 ml of 5% chromic acid. Maceration of the tissue was usually complete in 3-5 days at room temperature with occasional shaking on a variable speed whirl mixer. (In the younger tissue there was a tendency for incomplete maceration. When aggregations of cells were thus encountered the count was disregarded). No evidence of cell wall destruction nor loss of intracellular components was observed during this process. The cell suspension was diluted with 9% NaCl to between 10,000-40,000 cell/.5 ml and counted by a Model B Coulter Counter (Haileah Electronics). Tissue density was calculated subsequently.

RESULTS

The pattern of leaf growth for the duration of the experiment is shown in Figure 2. A logistic curve:

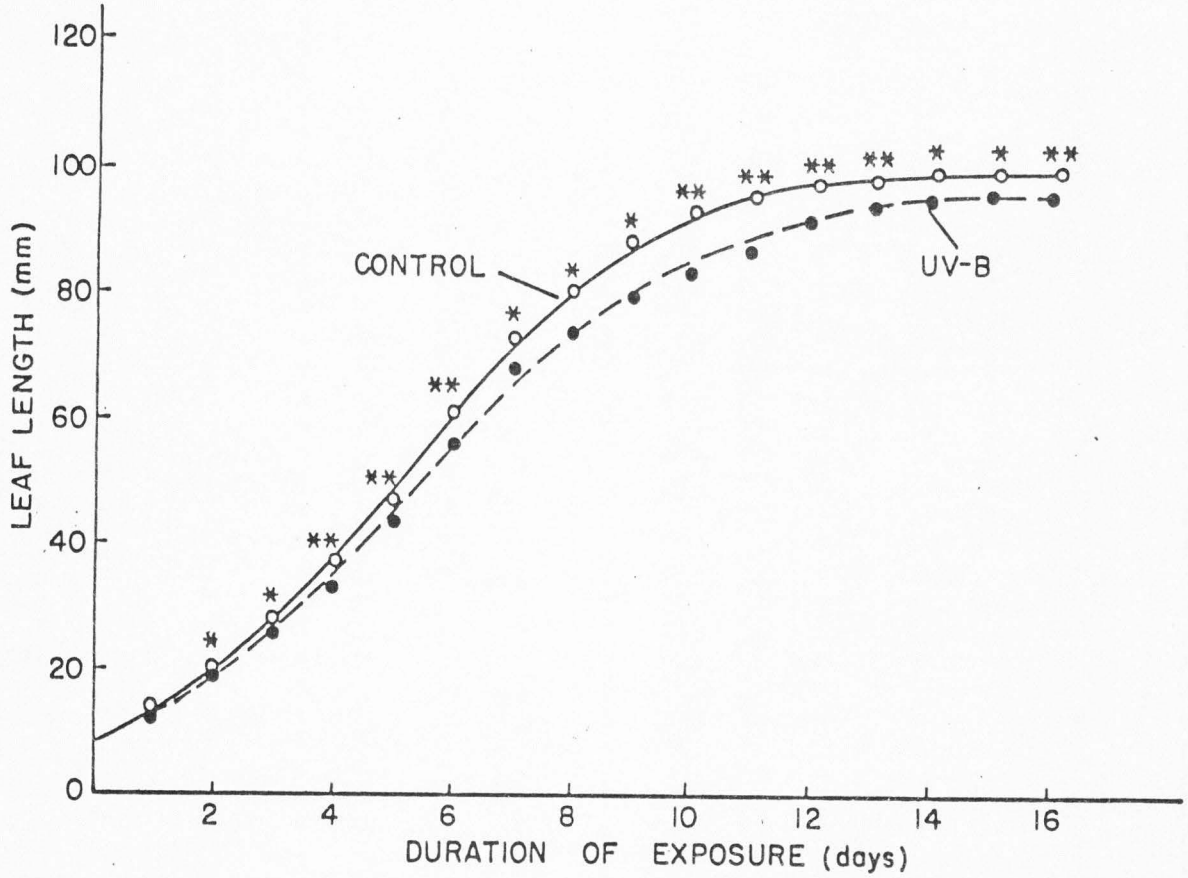

Figure 2. Leaf length for the fifth leaf of Rumex patientia L., during 16 days of UV irradiation (●——●) (equivalent to daily solar UV-B irradiation at 40° N latitude in mid-May with an atmospheric ozone concentration of 0.20 atm-cm) and control (○——○) treatment. Irradiation between 400 and 700 nm was 750 μeinsteins $m^{-2} \cdot s^{-1}$.

$$f(x) = \frac{1}{\frac{1}{l_m} - \left(\frac{1}{l_m} - \frac{1}{l_i}\right) e^{-rt}}$$

where:

l_m = maximal length
l_i = initial length
r = growth rate
t = time

was fitted to both sets of data. It seems that under enhanced UV-B radiation, plants had significantly shorter blades ($p<0.01$ for days 4,5,6,10,11,12,13 and 16; $p<0.05$ for days 2,3 and 9; $p<0.10$ for days 7,8,14 and 15) than those in the control treatment based on the t-test statistic for paired samples. This response occurred early (day 2) in the course of the experiment and is consistent with data provided by Sisson and Caldwell (1976). In addition the fitted logistic curve predicts that control leaves grew significantly faster ($p<0.001$) and achieved a larger final size ($p<0.10$), than those in the enhanced UV-B environment. The experiment was terminated at day 16 at which time the leaves from the six remaining plants showed no further growth gain and were assumed to have reached mature size.

The average size of two distinct cell types as determined by measurement in two dimensions is shown in Figure 3. Data from three locations in the leaf (tip, middle and base) were combined through a process which maximized the coefficient of determination, r^2. The justification for this combination is based on the assumption that the pattern of growth and differentiation is identical for all areas of the leaf but offset in time. The initiation and termination of this sequence begins first in the tip and midvein and last in the base and lamina portions of the leaf. The sole purpose of the

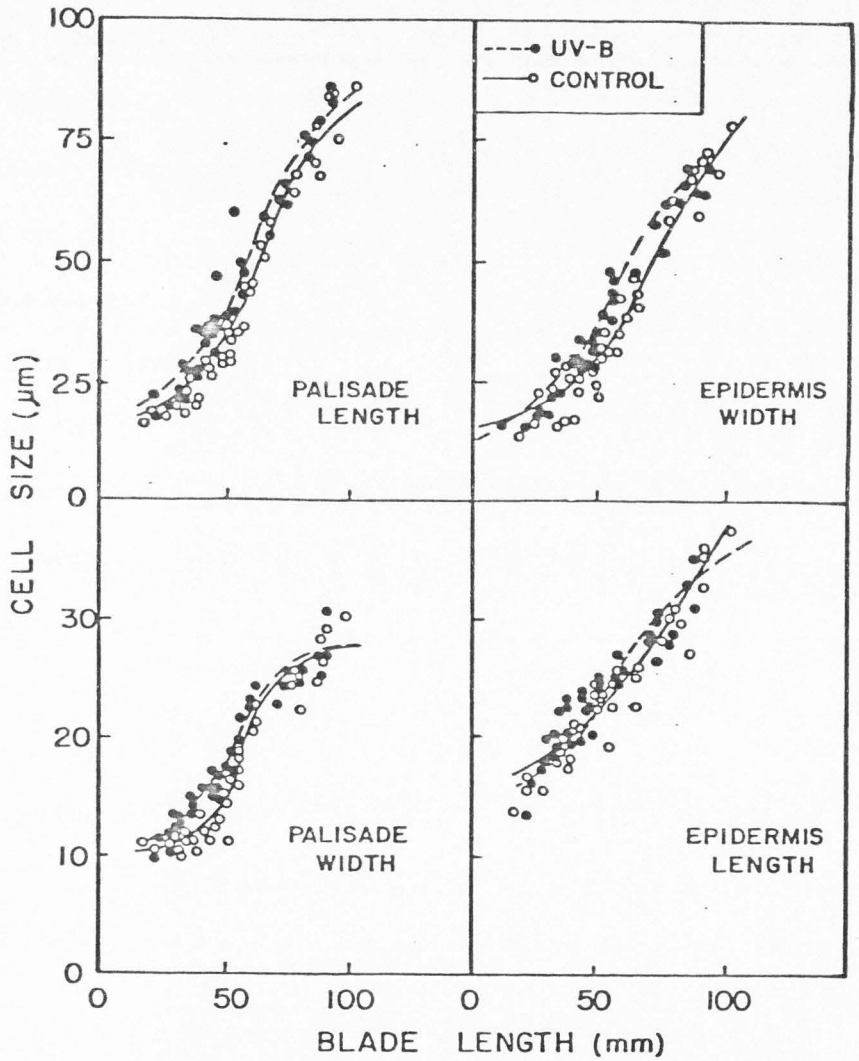

Figure 3. Cell size of the palisade mesophyll and upper epidermis of the fifth leaf of Rumex patientia L. exposed to UV-B irradiation (●— —●) (equivalent to daily solar UV-B radiation at 40°N latitude in mid-May with an atmospheric ozone concentration of 0.20 atm-cm) and control (o——o) treatment. Cell length is measured perpendicular to the plane of the blade, while width is measured parallel to the plane of the blade.

manipulation was to simplify both the presentation and interpretation of the data, while conserving the information.

For each data set, the logistic curve giving a minimum mean square error was fitted. Mean and standard error of initial and final cell size and slope (growth rate) of the computed curves were estimated during this process. These parameters were then subjected to statistical testing. Based on the t-test statistic, neither the initial nor the final cell dimension estimates were significantly different ($p>0.10$) for any of the four pairs. The slopes were, however, significantly different ($p<0.01$ for palisade length, palisade width and epidermis length; $p<0.10$ for epidermis width). Thus, it is apparent that under UV-B radiation enhancement, cell size increases earlier than in the control regime. This implies that there is possibly an earlier introduction of the cell expansion phase of leaf growth in this treatment.

The cell density data are shown in Figure 4. This again is a composite graph using data from the three areas of leaf tissue. A power curve

$$f(x) = ae^{bx}$$

where:

a = maximal intercept

b = slope

was fitted to each of data yeilding estimates for intercept and slope. Use of the t-test statistic showed that though the intercepts are not significantly different ($p>0.10$), the slopes are ($p<0.001$). These data suggest an earlier decrease in cell density of UV-B treatment plants when compared to control plants at any blade length and are consistent with those data describing cell size. It is reasonable to

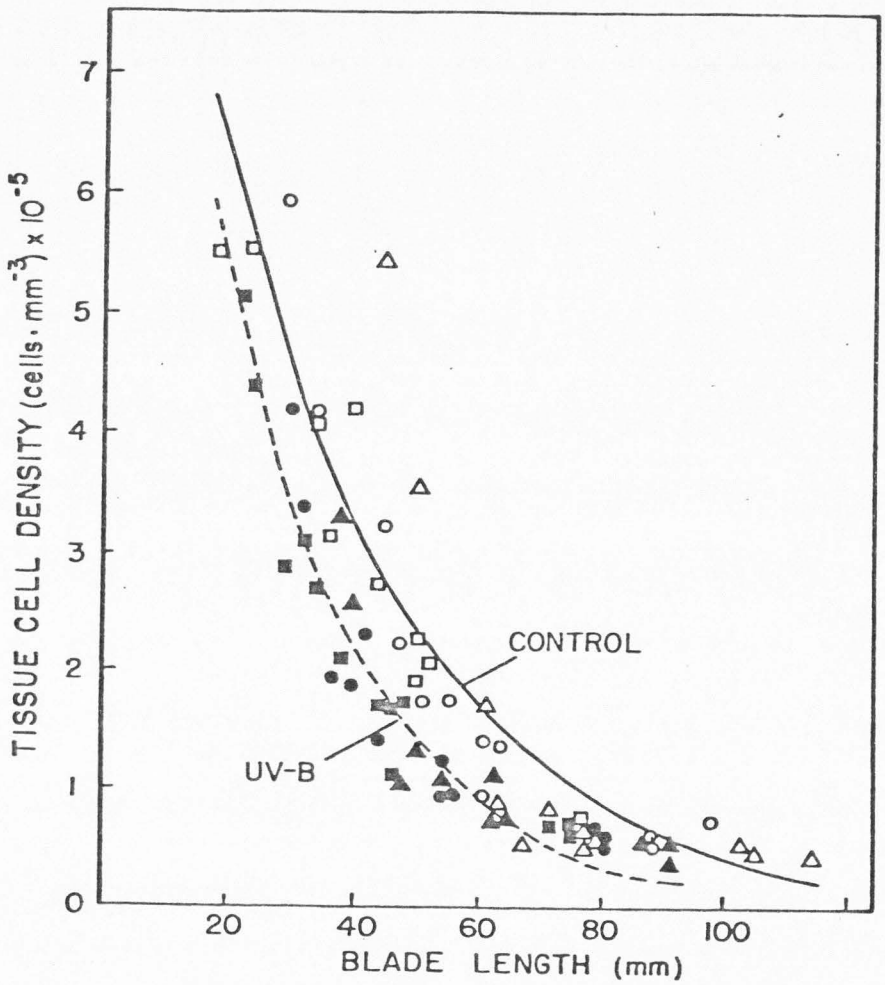

Figure 4. Tissue cell density of the fifth leaf of Rumex patientia L. exposed to UV-B irradiation (■--●--▲) (equivalent to daily solar UV-B radiation at 40°N latitude in mid-May with an atmospheric ozone concentration of 0.20 atm-cm) and control (□—○—△) treatments. The symbols △, ○ and □ refer to data collected from tissue in the tip, middle and basal portions of the leaf, respectively.

expect that tissue would have a lower cell density earlier in the UV-B treatment plants if in the same tissue, individual cells were expanding sooner.

DISCUSSION

Two factors which affect leaf ontogeny and ultimate leaf size: (1) the rate and duration of cell expansion and (2) the rate and duration of cell division, were examined for their role in the slowed early growth rates and smaller ultimate leaf size when plants are exposed to UV-B radiation.

The eventual size of the cells in a mature leaf depends on the degree to which cell expansion is influenced by (1) turgor pressure, (2) wall extension and new wall synthesis, (3) respiration, (4) continual synthesis of RNA and protein, and (5) auxin and other growth regulators (Cleland, 1958; 1971; Heyn, 1940; Tagawa and Bonner, 1957). Due to its potential to depress photosynthesis, UV radiation may indirectly influence the structure of the leaf through limiting the supply of energy for these processes. Ultraviolet radiation may also affect the normal activity of auxin since it is a UV-chromatophore (Giese, 1964; Curry et al., 1956).

If it is assumed that with UV-B irradiation the rate and duration of cell division proceed normally, but the rate (yet not the ultimate extent) of cell expansion is reduced, one might expect patterns of growth similar to those shown in Figure 5A. The increase in cell size and decrease in tissue cell density would lag behind that of the control plant growth, instead of preceeding as the present data suggest (Figures

3 and 4). In addition, the hypothesized pattern of blade growth (Figure 5A) which predicts that mature leaves from both treatments would reach the same size is not consistent with the observed pattern (Figure 2) in which mature leaf size differed significantly.

If, rather than the rate, the duration or extent of cell expansion was reduced by UV-B radiation while all other processes were unchanged, one would expect to observe data as suggested in Figure 5B. Cells in mature leaves would be smaller, on the average, and tissue would, therefore, have a greater final cell density in the UV-B treatment plants. This prediction is not in agreement with the pattern observed, where mature cell size and tissue cell density were not found to differ significantly between treatments (Figures 3 and 4).

If the rate at which cell division occurs is reduced by the irradiation, the growth pattern would likely be that pictured in Figure 5C. When the period of division is prolonged, fewer cells are in the process of dividing at any given time. As normal leaf unfoldment proceeds, more cells cease dividing and undergo expansion and differentiation. Therefore the average cell size would begin increasing before that in control plants. Accordingly, tissue cell density would decrease earlier. The result would be fewer cells in the leaf and, therefore, a smaller mature leaf size. The model predicted by this hypothesis is in agreement with the data presented (Figures 2, 3 and 4).

The rate at which cell division occurs is determined generally by the sequence of DNA replication, spindle formation and cell expansion. As it is known that DNA, RNA and proteins are UV-B chromatophores (Giese, 1964), these are possible targets for UV radiation. The

inhibition of cell division by UV radiation has been demonstrated (Cleaver, 1965; 1967; Domon and Rauth, 1968; Bootsma and Humphrey, 1968; Han et al., 1971; Carlson, 1976a,b). These researchers observed that the rate of cell division was most sensitive to UV radiation during the replication phase.

The duration of the cell division phase in leaves is a variable character and differs between species. Cessation can occur when leaves are *1/5-1/6, 1/4-1/3, 1/3-1/2* or *1/5* of final size for tobacco (Avery, 1933), cucumber (Milthorpe and Newton, 1963), spinach (Saurer and Possingham, 1970), and cocklebur (Maksymowych and Erickson, 1960), respectively. Division following unfoldment appears to be independent of the intensity of photosynthetically active radiation (Milthorpe and Newton, 1963). However, there exists the possibility that UV-B radiation may inhibit division during unfoldment and thereby reduce the number of cells and thus, the ultimate size of the mature leaf.

When comparing the observed data with those predicted by the models of leaf growth in terms of cell size, tissue cell density, and blade length, it is reasonable to refute the possibility that some modification of the processes of cell expansion, either in its rate or duration, is responsible for reduced leaf growth in UV irradiated plants. On the other hand, the data strongly indicate that the decreased rate of leaf growth observed under enhanced UV-B radiation is influenced primarily by an alteration in the cell division process.

A corroboration of the conclusion may be gleaned from the pattern of leaf development normally expected in plants. The number of cells in the leaf primordium affects ultimate leaf size. It has been shown that

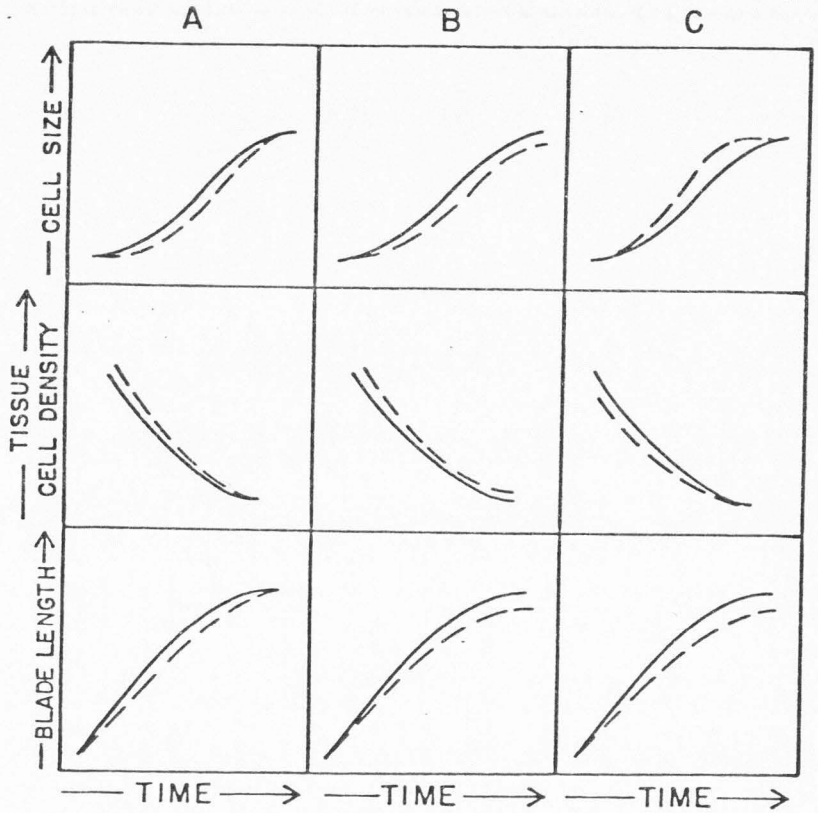

Figure 5. Models of hypothesized growth patterns as expressed in cell size, tissue cell density, and total blade length for leaves exposed to UV-B irradiation (----) and control (———) treatments. (For an explanation of hypotheses A, B and C, see text).

this number is dependent upon the intensity of visible radiation (cell number increases with increasing intensity) and the position of the leaf along the vegetative axis (Milthorpe and Newton, 1963). Typically, the first true leaves of a plant (e.g. Helianthus, Sunderland, 1960; Spinacea, Saurer and Possingham, 1970; and Rumex, personal observation) show a slower relative growth rate and reach a smaller mature size than later leaves on the same plant. This pattern is a function of fewer cells in the primordium (Milthorpe and Newton, 1963). The cells in these first true leaves eventually attain a size and shape similar to those in the later leaves, but due to fewer initial number of cells, the leaves are smaller.

Plants exposed to UV-B radiation exhibit a similar pattern of growth. Cell size and shape are comparable in mature leaves of both UV-B and control treatments (Figures 2,3, and 4). If the analogy holds, one can thus conclude that leaves of plants exposed to UV-B radiation, like the first true leaves of normal plants not subjected to UV-B radiation, are limited in size and in growth rate by a smaller total number of cells due to fewer cell division. In the UV radiation experiment, the number of cells in the leaf primordium for both treatments should have been the same since all plants received the same pretreatment. Therefore, it is assumed that the difference between treatments was a product of fewer cell divisions in the UV-B treatment plants during leaf unfoldment.

Further experimentation may yield evidence which would enable us to determine whether the UV radiation acts to reduce the rate or the duration of cell division. Preliminary observation of the frequency of mitosis in leaves of both UV-B and control treatments indicates that

the duration of the cell division phase does not differ. Mitotic frequencies were similar in both control and irradiated leaves, i.e., 32%, 24%, 7% and 0%, approximately, for harvest days 3,4,6 and 16, respectively.

The ecological implication of reduced leaf growth by enhanced UV-B radiation would seem clear. Smaller leaf area would reduce carbon fixation by the plant which in turn would result in less plant biomass and may alter competitive effectiveness. An understanding of the mechanism involved in UV-B radiation impairment of leaf growth should greatly facilitate prediction of how this stress may interact with other stresses to which plants are normally subjected.

LITERATURE CITED

Avery, G.S., Jr. 1933. Structure and development of the tobacco leaf A. J. Bot. 20:565-592.

Bener, P. 1972. Approximate values of intensity of natural ultraviolet radiation for different ammounts of atmospheric ozone. Final Technical Report, European Research Office, U.S. Army. London. Contract No. DAJA37-68-C-1017. 59 p.

Bootsma, D. and R.M. Humphrey. 1968. The progression of mammalian cells through the division cycle following ultraviolet radiation. Mut. Res. 5:289-298.

Caldwell, M.M. 1971. Solar UV irradiance and the growth and development of higher plants. In. A.C. Giese (ed.), Photophysiology, pp. 131-177. Academic Press, New York.

Carlson, J.G. 1976 a. Mitotic effects of monochromatic ultraviolet radiation at 225, 265, and 280-nm on eleven stages of the cell cycle of the grasshopper neuroblast in culture. I. Overall retardation from the stage irradiated to nuclear membrane breakdown. Rad. Res. 68:57-74.

Carlson, J.G. 1976 b. Mitotic effects of monochromatic ultraviolet radiation at 225, 265, and 280-nm on eleven stages of the cell cycle of the grasshopper neuroblast in culture. II. Changes in the progression rate and cell sequence between the stage irradiated to nuclear membrane breakdown. Rad. Res. 68:75-83.

Cicerone, R.J., R.S. Stolarski and S. Walters. 1974. Stratospheric ozone destruction by man-made chlorofluoromethanes. Science 185: 1165-1167.

Cleaver, J.E. 1965. Investigation into the effects of ultraviolet light on the rate of deoxyribonucleic acid systhesis in mammalian cells. Biochem. Biophys. Acta 108:42-52.

Cleaver, J.E. 1967. The relationship between the rate of deoxyribonucleic acid synthesis and its inhibition by ultraviolet light in mammalian cells. Rad. Res. 30:795-810.

Cleland, R. 1958. A separation of auxin-induced cell wall loosening into its plastic and elastic components. Physiol. Plant. 11:599-609.

Cleland, R. 1971. Cell wall extension. Ann. Rev. Pl. Phys. 22:197-222.

Curry, G.M., K.V. Thimann, and P.M. Ray. 1956. The base curvature of Avena seedlings to the ultraviolet. Physiol. Plant. 9:429-440.

Domon, M. and A.M. Rauth. 1968. Ultraviolet irradiation of mouse L cells: effects on DNA synthesis and progression of cells through the cell cycle. Rad. Res. 35:350-368.

Giese, A.C. 1964. Studies on ultraviolet radiation action upon animal cells. In A.C. Giese (ed.), Photophysiology Acad. Press, New York. pp. 203-245.

Green, A.E.S., T. Sawada, and E.P. Shettle. 1974. The middle ultraviolet reaching the ground. Photochem. Photobiol. 19:251-259.

Grobecker, A.J., S.C. Coroniti, and R.H. Cannon. 1974. The effects of stratospheric pollution by aircraft. Climatic Assessment Program, U.S. Dept. of Transportation. Report No. DOT-TST-75-50. Nat. Tech. Info. Serv., Springfield, Virginia.

Han, A., W.K. Sinclair, and C.K. Yu. 1971. Ultraviolet light-induced division delay in synchronized Chinese hamster cells. Biophys. J. 11:540-549.

Hammond, A.L. 1975. Ozone destruction: problem scope grows, its urgency recedes. Science 187:1181-1183.

Heyn, A.N.J. 1940. The physiology of cell elongation. Bot. Rev. 6:515-574.

Johnston, H. 1971. Reduction of stratospheric ozone by nitrogen oxide catalysts from supersonic transport exhaust. Science 173:517-522.

Maksymowych R. and R.O. Erickson. 1960. Development of the lamina in Xanthium italicum presented by the plastochron index. Am. J. Bot. 47:451-459.

Milthorpe, F.L. and P. Newton. 1963. Studies on the expansion of the leaf surface III. The influence of radiation on cell division and leaf expansion. J. Expt. Bot. 14:483-495.

Molina, M.J. and F.S. Rowland. 1974. Stratospheric sink for chloro-fluromethanes: chlorine atom-catalyzed destruction of ozone. Nature 249:810-812.

Sass, J.E. 1958. Botanical microtechnique. Ames, Iowa State College Press. 228 p.

Saurer, W. and J.V. Possingham. 1970. Studies on the growth of spinach leaves (Spinacea oleracea). J. Expt. Bot. 21:151-158.

Sisson, W.B. and M.M. Caldwell. 1975. Lamp/filter systems for simulation of solar UV irradiance under reduced atmospheric ozone. Photochem. Photobiol. 21:453-456.

Sisson, W.B., and M.M. Caldwell. 1977. Photosynthesis, dark respiration, and growth of Rumex patientia L. exposed to UV irradiance (288-315 nm) simulating a reduced atmospheric ozone column. Plant Phys. 58:563-568.

Tagawa, T. and J. Bonner. 1957. Mechanical properties of the Avena coleoptile as related to auxin and to ionic interaction. Plant Phys. 38:207-212.

Van, T.K., L.A. Garrard, and S.H. West. 1976. Effects of UV-B radiation on net photosynthesis of some crop plants. Crop Sci. 16:715-718.

APPENDIX

APPENDIX

Table 1. Compilation of data used in calculation of tissue cell density.

		UV Treatment						Control Treatment					
	Position A=tip, B=mid C=base	# Cells/sample	x10^x	Thickness (mm)	Area (mm^2)	Volume mm^3	Blade length (mm)	# Cells/sample	x10^x	Thickness (mm)	Area (mm^2)	Volume mm^3	Blade length (mm)
DAY 3	A	1.88	6	.210	27	5.7		1.84	6	.190	18	3.4	
	B	3.40	6	.185	44	8.1		2.3	6	.185	21	3.9	
	C	3.08	6	.175	34	6.0		1.66	6	.145	21	3.0	
	TOTAL	8.36	6		105	19.8	22	5.70	6		60	10.3	18
	A	2.90	6	.250	43	10.8		2.38	6	.210	32	6.7	
	B	4.12	6	.230	53	12.2		3.96	6	.210	45	9.5	
	C	3.34	6	.200	38	7.6		3.64	6	.200	33	6.6	
	TOTAL	1.03	7		134	30.6	24	9.98	6		110	22.8	23
	A	2.07	6	.230	53	12.2		2.87	6	.230	75	17.5	
	B	3.80	6	.230	85	19.5		6.80	6	.200	106	21.2	
	C	4.00	6	.230	61	14.0		4.60	6	.175	64	11.2	
	TOTAL	9.87	6		199	45.8	29	1.43	7		245	49.7	34
DAY 4	A	3.43	6	.235	137	32.2		2.51	6	.235	123	28.9	
	B	4.70	6	.230	110	25.3		4.88	6	.220	121	26.6	
	C	6.46	6	.190	110	20.9		2.54	6	.200	41	8.2	
	TOTAL	1.46	7		357	78.9	32	1.09	7		285	63.7	36
	A	3.83	6	.210	103	21.6 21.6		1.62	6	.280	101	28.3	
	B	5.76	6	.210	120	25.2		5.88	6	.220	155	34.1	
	C	3.88	6	.215	67	14.4		5.50	6	.190	69	13.1	
	TOTAL	1.25	7		290	61.2	34	1.30	7		325	75.5	40
	A	3.18	6	.275	110	30.3		2.70	6	.280	120	33.5	
	B	4.56	6	.260	125	32.5		7.64	6	.260	172	44.7	
	C	5.92	6	.245	115	28.2		9.34	6	.235	145	34.1	
	TOTAL	1.37	7		350	91.0	38	1.95	7	.775	437	112.3	44
DAY 6	A	5.30	6	.345	143	49.3		4.98	6	.330	228	76.4	
	B	7.33	6	.300	202	60.6		1.39	7	.300	332	99.6	
	C	5.92	6	.250	200	52.0		9.32	6	.230	177	40.7	
	TOTAL	1.86	7		545	161.9	46	1.57	6		737	216.7	50
	A	3.92	6	.330	166	54.8		4.72	6	.355	224	84.0	
	B	8.15	6	.315	272	85.7		8.54	6	.305	296	90.3	
	C	1.01	6	.260	234	60.8		9.47	6	.265	187	49.6	
	TOTAL	2.22	7		672	201.3	46	2.27	7		707	223.9	50
	A	5.40	6	.325	230	74.8		4.46	6	.315	240	75.6	
	B	8.57	6	.310	289	89.6		1.20	7	.275	318	87.5	
	C	1.11	6	.290	224	65.0		7.44	6	.245	147	36.0	
	TOTAL	2.51	7		743	229.4	48	2.39	7		705	199.1	52
DAY 16	A	1.00	7	.400	436	174.4		1.12	7	.385	568	218.7	
	B	1.69	7	.365	672	245.3		1.80	7	.360	818	294.5	
	C	9.90	6	.330	425	140.3		1.44	7	.345	548	189.1	
	TOTAL	3.68	7		1533	560.0	71	4.36	7		1934	702.3	77
	A	8.78	6	.390	409	159.5		9.40	6	.420	467	196.1	
	B	1.53	7	.375	687	257.6		1.38	7	.385	720	277.2	
	C	1.24	7	.350	558	195.3		1.37	7	.375	538	201.8	
	TOTAL	3.65	7		1654	612.4	75	3.69	7		1725	675.1	78
	A	8.54	6	.420	521	218.8		8.88	7	.405	533	215.9	
	B	1.44	7	.395	683	269.8		2.82	7	.405	941	381.1	
	C	1.88	7	.375	657	246.4		2.46	7	.405	915	370.6	
	TOTAL	4.15	7		1861	735.0	75	6.17	7		2389	967.6	87

VITA

Judith Grace Dickson

Candidate for the Degree of

Master of Science

Thesis: Leaf Development of Rumex patientia L. Exposed to UV Irradiation (280-320 nm).

Major Field: Range Ecology

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