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Photosynthesis, Dark Respiration, and Growth of *Rumex patientia* L. Exposed to Ultraviolet Irradiance (288 to 315 Nanometers) Simulating a Reduced Atmospheric Ozone Column[1]

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WILLIAM B. SISSON[2] AND MARTYN M. CALDWELL
Department of Range Science and The Ecology Center, Utah State University, Logan, Utah 84322

ABSTRACT

Net photosynthesis, dark respiration, and growth of *Rumex patientia* L. exposed to a ultraviolet irradiance (288–315 nanometers) simulating a 0.18 atm·cm stratospheric ozone column were determined. The ultraviolet irradiance corresponding to this 38% ozone decrease from normal was shown to be an effective inhibitor of photosynthesis and leaf growth. The repressive action on photosynthesis accumulated through time whereas leaf growth was retarded only during the initial few days of exposure. Small increases in dark respiration rates occurred but did not continue to increase with longer exposure periods. A reduction in total plant dry weight and leaf area of approximately 50% occurred after 22 days of treatment, whereas chlorophyll concentrations remained unaltered.

Global UV irradiance on the earth's surface fluctuates with changes in solar altitude, cloud cover, stratospheric ozone concentration, and atmospheric turbidity. No appreciable UV radiation below 295 nm is received on the earth's surface due to absorption of UV radiation by the stratospheric ozone layer. A reduction of the stratospheric ozone column would result in a predictable shift in the terrestrial global spectrum to include shorter UV wavelengths below 295 nm (3, 13). Such a reduction could result from catalytic interactions of ozone with oxides of nitrogen released in the stratosphere by aircraft (14, 16), halomethanes diffusing from the troposphere (6, 15, 22) or other man-induced perturbations of the stratosphere. Although the resulting shift in the global UV radiation spectrum resulting from partial ozone reduction would be small (3, 13), any added increment of shorter wavelength UV radiation might prove significant since it is effectively absorbed by chromophores such as nucleic acids and proteins (11).

Historically, UV radiation photobiological research has dealt principally with monochromatic 254-nm radiation. From these studies, an array of deleterious effects on plants has been shown. These effects include such responses as reduced growth (25), inhibition of several component reactions of photosynthesis (1, 17, 20, 26), and stimulated dark respiration (24). Extrapolation of known plant responses to 254-nm radiation in assessing the quantitative ramifications of an enhanced component of UV radiation in the terrestrial global spectral irradiance due to partial ozone reduction does not, at the present time, appear plausible for three reasons. First, biological response to UV radiation tends to be highly wavelength-specific with respect to efficiency of photobiological action (5, 11). Second, the biologically potent waveband shorter than 280 nm would not be transmitted to the earth's surface even if the ozone column were reduced to 40% of its present thickness (13). Finally, there may be qualitative as well as quantitative differences in the response to 254-nm radiation and radiation in the 288- to 315-nm waveband as has been reported for *Chlamydomonas reinhardi* (23).

This paper reports on evaluation of net photosynthesis, dark respiration, and growth of *Rumex patientia* L. exposed to UV irradiation corresponding to the global UV spectral irradiance which would occur with partial ozone reduction. The level of ozone reduction simulated was approximately 38% from normal, and resulted in an almost immediate detrimental effect on those plant processes when assayed in both field and controlled environment studies.

R. patientia was selected as the test species for this study because: (*a*) it is reasonably sensitive to UV radiation as determined in preliminary studies evaluating approximately 20 native and agricultural plant species; (*b*) it is normally exposed to full sunlight in its natural habitat; and (*c*) individual leaves are relatively long lived (about 60 days) and are not normally shaded by other leaves of the same plant.

MATERIALS AND METHODS

Germination of *R. patientia* L. seeds was carried out in Petri dishes, and the seedlings were transplanted individually into peat pots and then into 10-cm pots at initiation of the first leaf. The plants remained in a greenhouse until full expansion of the third leaf. Temperatures in the greenhouse fluctuated between 20 C (night) and 35 C (day). From these, the most uniform appearing plants were selected for each controlled environment experiment. For field studies, the plants were transferred to field plots for approximately a week of equilibration under normal global irradiation prior to treatment. Only the most uniform appearing plants were selected for the experiment. In all experiments, the third leaf was used for photosynthetic determinations. Upon initiation of treatment, the plants were approximately 5 weeks old from the time of germination, and the third leaf was about 15 days old.

An 11-hr photoperiod with temperature programmed to simulate a July day in Logan, Utah (ranging from 13–37 C) was used in all controlled environment studies. The light source in the controlled environment experiments was a 6000-w Osram Co. xenon arc mounted below a parabolic reflector. The UV-radiation-enhanced treatment consisted of: (*a*) one layer of Mylar type A (10 mil) plastic film which enclosed the lamp and removed all UV radiation produced by the xenon arc below 315

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[2] Current address: Jornada Experimental Range, New Mexico State University, P.O. Box 698, Las Cruces, N. M. 88001.

nm; and (*b*) two Westinghouse FS-40 sun lamps each filtered by one layer of Kodacel TA-401 (5 mil) plastic film which provided supplemental UV irradiation corresponding to a 0.18 atm·cm stratospheric ozone column at a solar altitude of 60° (27). The normal level of ozone in August in northern Utah (42°N, 112°W), where this population of *Rumex* was collected, is approximately 0.29 atm·cm (27).

The FS-40 sun lamps produce mercury vapor emission lines at 365, 404, and 436 nm (27). Klein *et al.* (18) showed that 365-nm irradiance repressed vegetative growth of plants. Although the 365-nm wavelength is evident in the spectral irradiance of the FS-40 lamp (0.06 $w \cdot m^{-2}$ at 9.2-cm distance), these lamps provide a comparatively small addition of 365-nm radiation to the 360- to 370-nm waveband already present in irradiation from the sun (approximately 5 $w \cdot m^{-2}$, at a solar altitude of 60°) or the xenon arc (approximately 2.2 $w \cdot m^{-2}$, when the lamp is operating at 800 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$ PAR).[3] Nevertheless, so that differences in plant response to the UV radiation and control treatments could be attributed solely to the supplemented UV radiation in the 288- to 315-nm waveband, the control treatment also consisted of two FS-40 sun lamps, each filtered with one layer of Mylar type A (10-mil) plastic film. This filter effectively absorbs all UV radiation below 315 nm, but has transmission characteristics similar to Kodacel film above 315 nm.

In field studies, UV radiation simulating a 0.18 atm·cm ozone column was also evaluated. As previously described for the controlled environment studies, two FS-40 sun lamps, each filtered by Kodacel TA-401 (5-mil) or Mylar type A (10 mil) plastic film filters, were used for the UV radiation and control treatments, respectively. Spectral irradiance resulting from solar radiation with supplemental UV radiation below 315 nm (0.18 atm·cm ozone simulation) and with the control lamp system (0.29 atm·cm ozone) is shown in Figure 1. These measurements were made when the solar altitude was 60° during a cloudless day with a Gamma Scientific Co. spectroradiometer. Photosynthetically active radiation was 2150 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$. The lamp/filter systems were used daily when the solar altitude exceeded 40°.

Net photosynthetic rates of single leaves were determined with a Siemens Corp. gas exchange system (19), and IR gas analyzer (Beckman Co.) (8). Leaf diffusive resistances were measured and calculated by a modification of the technique of Gaastra (10). A multiplier (1.594) which relates the diffusion coefficients of CO_2 and H_2O (21) was used to calculate CO_2 diffusive resistances from the H_2O diffusive resistances. In this study, the CO_2 mesophyll resistance originally defined by Gaastra (10) was replaced by the residual resistance term, since this includes all diffusive and metabolic components of the total CO_2 resistance apart from stomatal and boundary layer resistances (12).

In this study, PAR is the quantum flux between 400 and 700 nm (μeinsteins $\cdot m^{-2} \cdot sec^{-1}$) considered as photosynthetically active radiation and measured with a Lambda Co. model LI-190SR quantum sensor (4). Air and leaf temperatures within the gas exchange cuvette were measured with platinum wire resistance thermometers and fine-wire thermocouples, respectively. A Cambridge model 880 dew point hygrometer measured water vapor concentrations. Specific water vapor concentrations of the incoming cuvette air stream were achieved by mixing two air streams of different water vapor concentrations. Leaf areas were measured with a Lambda model LI-3000 portable area meter. Photosynthesis is expressed on a leaf area (one side) basis. Dry weight determinations were made after oven drying at 42 C for 2 days.

Photosynthetic rates of plants from both the field and controlled environment studies were determined in the Siemens cuvette with a UV enhanced spectral irradiance corresponding to that used in the respective experiments. For the plants subjected to UV radiation enhancement, the normal cuvette cover was replaced with one layer of Kodacel TA-401 (5 mil) plastic film filter, and two Westinghouse FS-20 sun lamps provided the desired UV radiation supplement to simulate a 0.18 atm·cm ozone column. Four incandescent Sylvania 300-w lamps provided irradiation above 315 nm. These lamps were adjusted to simulate the total PAR quanta used in the controlled environment experiments. Photosynthetic determinations for the field experiment plants were made at 800 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$ PAR. Total PAR quanta were monitored in the cuvette by a Lambda model LI-190SR quantum sensor (4). A constant temperature of 27 C was maintained in the cuvette with 45% (±4%) relative humidity during all photosynthetic determinations.

Chlorophyll concentrations were determined on both a fresh and dry weight basis by the method of Arnon (2).

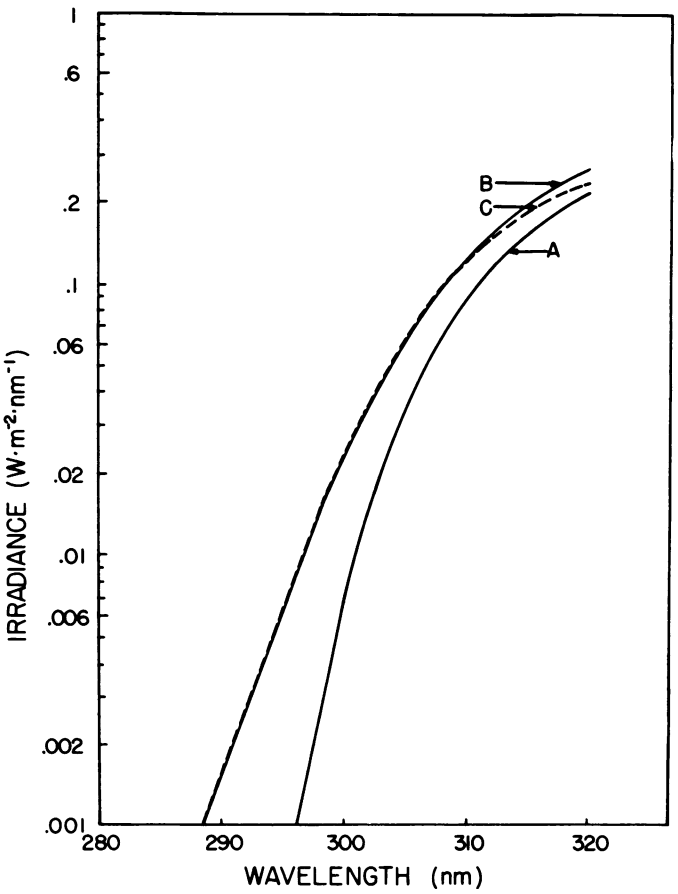

FIG. 1. Spectroradiometer measurements of global irradiance with the sun at an altitude of 60° supplemented with two FS-40 lamps each filtered with: (A) Mylar type A 10-mil (0.25-mm) plastic film yielding the control ozone concentration of 0.29 atm·cm; (B) Kodacel TA 401 5-mil (0.13-mm) plastic film simulating a 0.11 atm·cm stratospheric ozone decrease. Curve C represents the predicted spectral irradiance at 0.11 atm·cm stratospheric ozone decrease from a base level of 0.29 atm·cm (from Sisson and Caldwell [27]).

RESULTS

Controlled Environment Studies. Net photosynthetic rates of *R. patientia* over a 7-hr period were determined to measure the initial short term effects of a UV enhanced irradiance simulating a 0.18 atm·cm ozone column. The visible part of the spectrum

[3] Abbreviation: PAR: photosynthetically active radiation (400–700 nm).

was maintained at 400 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR. Consistent, significant differences ($P < 0.05$) between the UV radiation and control treatments were found after a 2-hr exposure (Fig. 2). Mean net photosynthetic rates of the UV-radiation-treated plants were depressed 15% below the control plants after a 7-hr treatment. This difference was still apparent after a 10-hr dark period. Although total CO_2 resistance was significantly greater for the plants exposed to UV irradiance, the variability exhibited by the components of the total CO_2 resistance eliminated statistically significant differences ($P < 0.05$) between treatments (Fig. 2). The leaf resistance component ($r'_a + r'_s$) appeared to be more responsible for the significant increase in total CO_2 resistance than did the residual component (r'_r). This would suggest an effect on stomatal aperture. Zill and Tolbert (29) similarly observed a 30 to 50% stomatal closure in Thatcher wheat after 30 min of intense 254-nm radiation (3.5 w$\cdot m^{-2}$).

Net photosynthetic rate determinations over a 7-day period under the same UV enhanced irradiance and visible irradiance as used in the previous short term study (400 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR) are presented in Figure 3. Net photosynthetic rates of the UV-radiation-treated plants were significantly ($P < 0.05$) reduced after one 11-hr day of treatment. Leaf resistances ($r'_a + r'_s$) did not differ significantly ($P < 0.05$) between treatments, whereas the residual resistances (r'_r) were found to be significantly ($P < 0.05$) different after 1 day of UV radiation exposure (Fig. 3). The decreasing photosynthetic rates and increasing r'_r observed in the control plants over time were probably due to

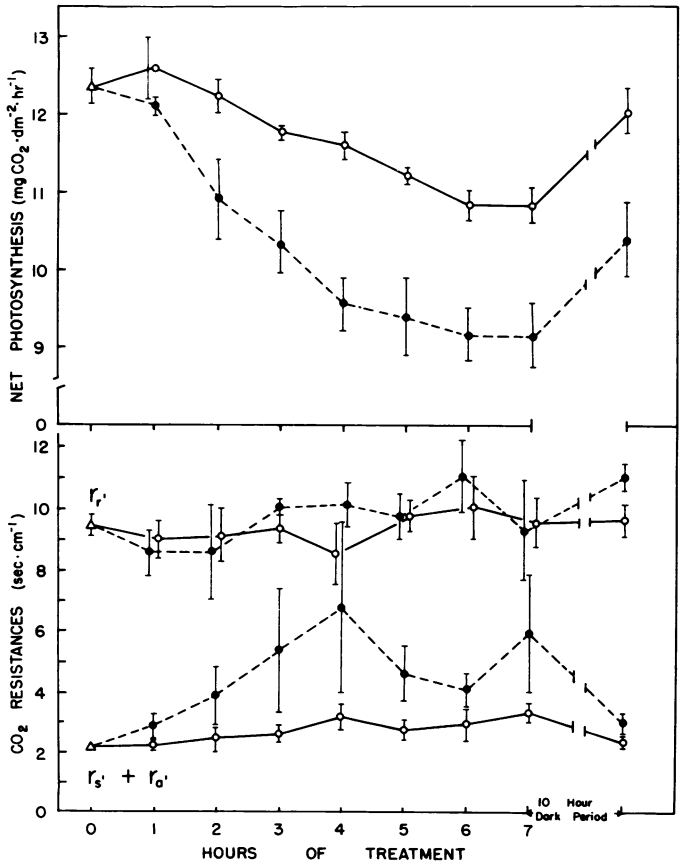

FIG. 2. Net photosynthesis and the associated CO_2 resistances (r'_r: residual resistance; $r'_s + r'_a$: leaf resistance) of the third leaf of *R. patientia* L. for 7 hr of UV irradiance (●- - -●) (simulating a 0.18 atm·cm stratospheric ozone level at a solar altitude of 60°) and control (O——O) treatment. PAR irradiance was 400 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$. Vertical bars represent ± one standard error and each point is the mean of five replicates.

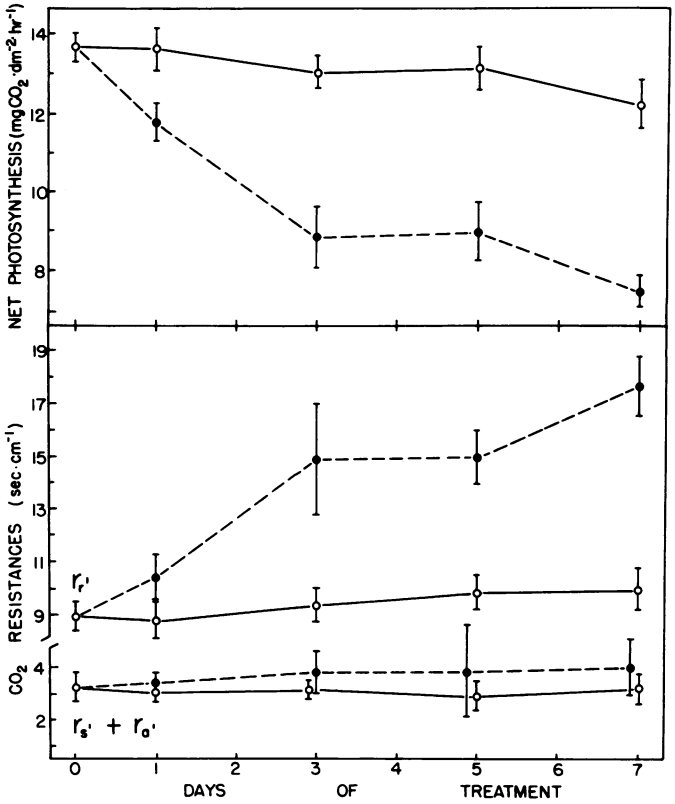

FIG. 3. Net photosynthesis and CO_2 resistances (r'_r: residual resistance; $r'_s + r'_a$: leaf resistances) of *R. patientia* L. during 7 days of UV irradiance (●- - -●) (simulating a 0.18 atm·cm stratospheric ozone level at a solar altitude of 60°) and control (O——O) treatment in controlled environment studies. PAR irradiance was 400 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$. Vertical bars represent ± one standard error and each value is the mean of four or five replicates.

increasing leaf age since the same leaves (third leaf) were used for photosynthetic determinations throughout the study.

Photosynthetic rates of *R. patientia* under the same UV enhanced irradiance, temperatures, and photoperiod as the previous experiment but with 800 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR yielded essentially the same results (Fig. 4). These experiments were conducted at two levels of PAR (400 and 800 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$) to determine if the effects of UV irradiation would be more severe at a lower visible irradiance when light for photosynthesis and photorepair processes might be more limiting. However, comparable cumulative UV radiation repression of photosynthesis is suggested for both visible irradiance experiments through 7 days of exposure. In addition, an almost identical response was noted for the calculated r'_r and $r'_a + r'_s$ resistances in both the 400 and 800 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR experiments. That is, no statistically significant ($P < 0.05$) differences were found between the UV irradiated and control plants for $r'_a + r'_s$, whereas r'_r differed statistically after 1 day of treatment. Stomatal aperture did not appear to be affected in the longer term UV-radiation-enhanced treatments (at either 400 or 800 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR), as was suggested to occur in the short term (7-hr) exposure study.

Dark respiration rates determined in this experiment (800 μeinsteins$\cdot m^{-2}\cdot sec^{-1}$ PAR experiment) were significantly ($P < 0.05$) higher in the UV-radiation-enhanced treatment (Fig. 4). Owen (24) reported that short term exposure of tobacco plants to 254-nm radiation (8.7 w$\cdot m^{-2}$) also resulted in increased dark respiration and furthermore, that longer UV radiation exposure caused continued increases in respiration rates. In our study, a

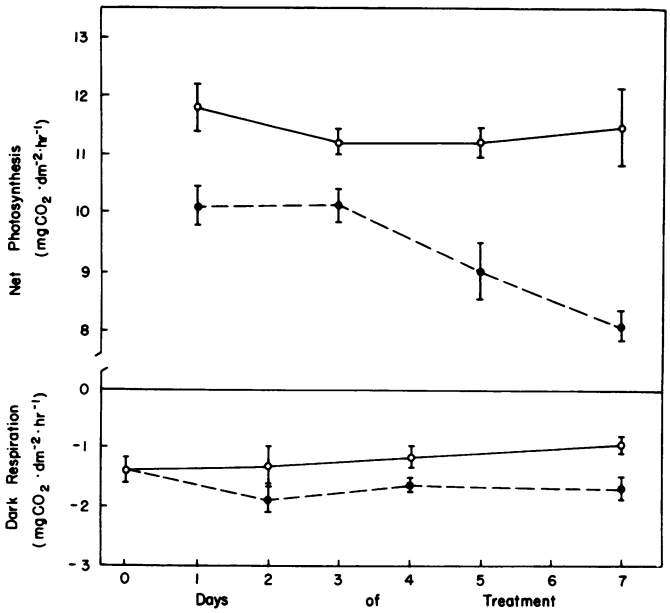

FIG. 4. Net photosynthesis and dark respiration of *R. patientia* L. during 7 days of UV irradiance (●- - -●) (simulating a 0.18 atm·cm stratospheric ozone level at a solar altitude of 60°) and control (○——○) treatment in controlled environment studies. PAR irradiance was 800 μeinsteins·m^{-2}·sec^{-1}. Vertical bars represent ± one standard error and each point is the mean of four to six replicates.

relatively stable elevated dark respiration rate was maintained through 7 days of UV radiation exposure.

Leaf length measurements for the 800 μeinsteins·m^{-2}·sec^{-1} PAR experiment are shown in Figure 5. Leaf lengths for each leaf were compared between treatments for each day beginning at leaf initiation. Consistent, significant ($P < 0.05$) differences were found after 3 days of treatment in leaf 1, and 2 days for leaves 2 to 6. As shown in Figure 5, leaf length and time of leaf exertion were retarded for leaves 2 through 6 when plants were exposed to the enhanced UV irradiance. Upon termination of this study, dry and fresh weights for above ground biomass and total leaf area were determined (Table I). Mean values of the UV-radiation-treated plants were less than 50% of the control plants, and all parameters differed significantly ($P < 0.01$) between treatment and control. Fresh and dry weight to leaf area ratios were similar between treatments (Table I). Total Chl concentrations did not differ significantly ($P < 0.05$) between treatment and control on a dry weight basis (Table I).

Field Study. Net photosynthesis was determined for *R. patientia* in a field experiment under a UV enhanced global spectral irradiance corresponding to a 0.18 atm·cm ozone column (Fig. 6). Under these conditions, significantly ($P < 0.05$) depressed photosynthetic rates were found for the UV enhanced treatment plants after 4 days. The calculated CO_2 resistances (Fig. 6) followed similar trends as those of plants treated similarly in controlled environment experiments.

DISCUSSION

The UV enhanced irradiance corresponding to a 0.18 atm·cm ozone column resulted in almost immediate suppression of photosynthesis and leaf expansion of *R. patientia*. Decreased photosynthesis could be detected after only 2 hr of exposure to the UV irradiance. Partial stomatal closure was implicated in the suppression of photosynthesis during the initial exposure to UV radiation. After 1 day of exposure, leaf resistances (r'_a and r'_s) did not differ between UV irradiated and control plants, indicating that stomatal diffusion resistance was not involved in the lower photosynthetic rates of the UV irradiated plants. The effects of the UV irradiation must, therefore, have involved other components of the photosynthetic apparatus apart from stomatal diffusion, as indicated by the increased residual resistance term.

Unlike earlier reports of Chl destruction by intense 254-nm

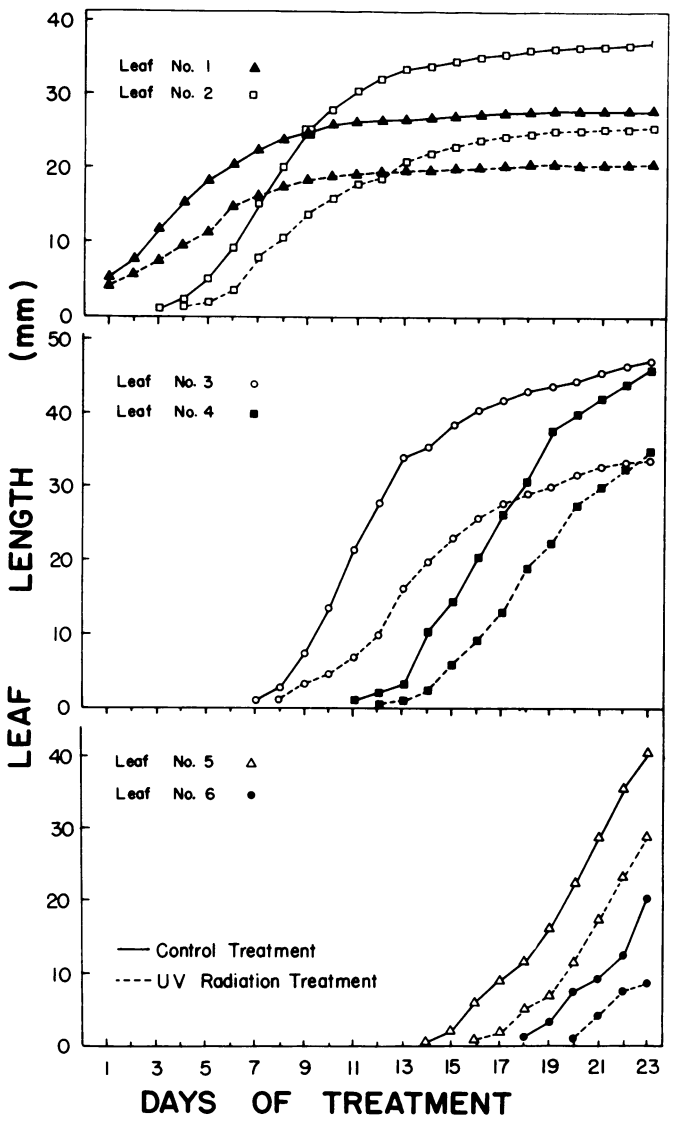

FIG. 5. Leaf length for leaves 1 through 6 of *R. patientia* L. during 23 days of UV irradiance (- - -) (simulating a 0.18 atm·cm stratospheric ozone level at a solar altitude of 60°) and control (——) treatment in controlled environment studies. PAR irradiance was 800 μeinsteins·m^{-2}·sec^{-1}. Each point represents the mean of six replicates.

Table I. Mean dry and fresh weight for aboveground biomass, total leaf area, fresh and dry weight to leaf area ratios, and total chlorophyll of Rumex patientia

Total chlorophyll values represent the mean of 6 replicates of leaves 1 through 6. All other values are the mean of 6 replicates. These measurements were made after 23 days of UV irradiation(simulating a 0.18 atm·cm ozone column; 60° solar altitude) and control treatments in controlled-environment studies. PAR irradiation was 800 μeinsteins·m^{-2}·sec^{-1}.

	UV radiation treatment	Control treatment
Leaf area (cm^2)	44.79	89.67**
Fresh weight (g)	1.37	2.99**
Fresh weight/leaf area	0.030	0.033
Dry weight(g)	0.13	0.29**
Dry weight/leaf area	0.003	0.003
Total leaf chlorophyll(mg chl·g dry wt^{-1})	14.98	14.48

** Represents significant differences at P<.01.

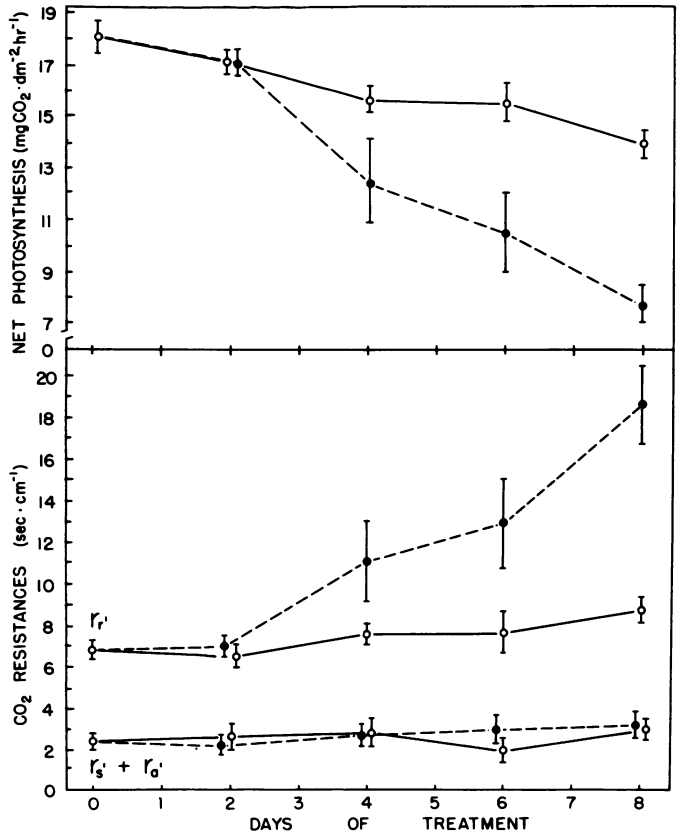

FIG. 6. Net photosynthesis and CO_2 resistances (r'_r: residual resistance; $r'_s + r'_a$: leaf resistance) of *R. patientia* L. during 8 days of UV irradiance (●- - -●) (simulating a 0.18 atm·cm stratospheric ozone level at solar altitude of 60°) and control (○——○) treatment in field studies. Vertical bars represent ± one standard error and each point is the mean of four to six replicates.

radiation (7, 9), Chl concentrations were not depressed by irradiance in the 288- to 315-nm waveband. If UV irradiance in this waveband has the potential to destroy Chl similar to 254-nm radiation, the intensities, exposure periods, or both were insufficient to cause destruction in this study. Thus, the repressed photosynthetic rates of the UV irradiated plants were not a secondary effect of Chl destruction.

Photoreactivation involves a partial or complete repair of molecular damage induced by UV irradiation. This repair is dependent on radiation of longer wavelengths (315–550 nm). A variety of deleterious physiological manifestations of UV irradiation (primarily 254-nm) in higher plants has been shown to be photoreactivable (5, 24). Conclusive evidence that impairment of photosynthesis by UV radiation is photoreactivable has not been found, although this is suggested by Van Baalen (28) in his experiments with blue-green alga. Apart from photoreactivation, visible radiation may also contribute to the repair or replacement of damaged organelles or tissues. After 3 days of exposure, photosynthesis in the UV irradiated plants of the low PAR experiment (400 μeinsteins·m^{-2}·sec^{-1}) was depressed to 68% of control plant photosynthesis, whereas rates of the UV irradiated plants in the high PAR experiment (800 μeinsteins·m^{-2}·sec^{-1}) were still 90% of control plant rates. However, after 7 days of UV radiation exposure, photosynthesis of the UV irradiated plants in the high PAR experiment was depressed almost as much as in the low PAR experiment (70 and 62% of control plants, respectively). Although UV radiation did appear to be more effective in depressing photosynthesis when visible light intensities were low, this effect appeared to be pronounced only during the earlier stages of treatment.

Under conditions of either high or low PAR light, the depressive effects of UV irradiation on photosynthesis appeared to accumulate with continued exposure. Although plants in these experiments were exposed to UV radiation corresponding to a sizable depletion of atmospheric ozone (38% reduction), even with only a 5 or 10% ozone reduction, the effects of this increased UV irradiance could be significant for plants with reasonably long lived leaves if the damage accumulates in a manner similar to that demonstrated in these experiments. Experiments presently underway suggest that photosynthesis and growth of *R. patientia* are somewhat depressed when exposed to UV-B irradiation under prevailing August ozone concentrations (0.29 atm·cm; 60° solar altitude) as compared to plants exposed to irradiance completely devoid of wavelengths shorter than 315 nm. Thus, even small reductions in ozone concentrations (*e.g.* 5 or 10%) would be expected to reduce further the efficiency of plant processes such as plant growth and photosynthesis.

Photosynthetic rates of the UV irradiated plants in the field experiment did not show a significant depression until after 4 days, whereas those treated similarly in the controlled environment experiment were significantly repressed after 1 day (Figs. 3, 4, and 6). This may have resulted from the absence of UV-B radiation in the control treatment of the growth chamber experiment, whereas in the field, control plants were exposed to normal ambient UV-B irradiation.

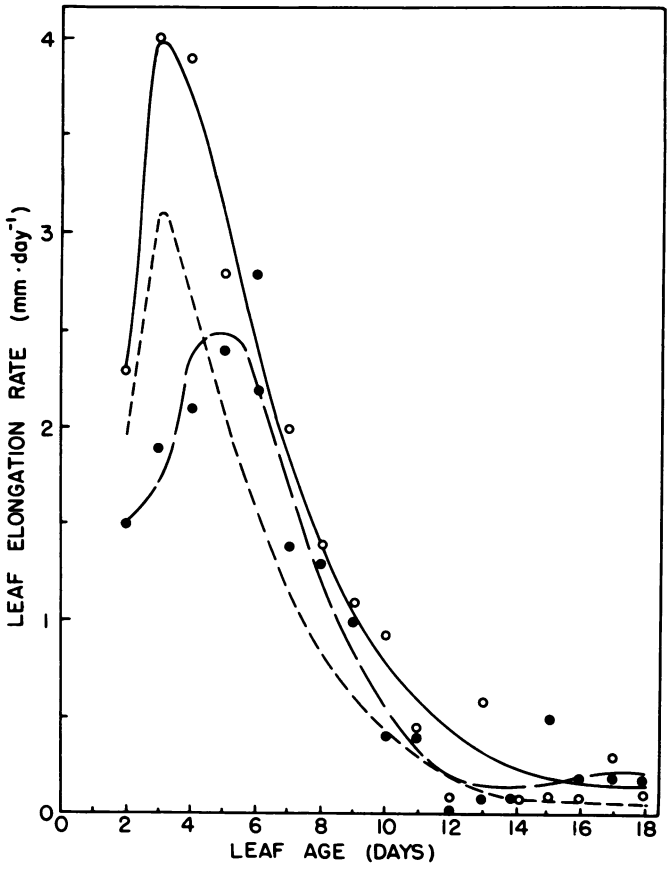

FIG. 7. Leaf elongation rates (mm·day^{-1}) of the first leaf of *R. patientia* L. during 18 days of UV irradiance (●) (simulating a 0.18 atm·cm ozone column at a solar altitude of 60°) and control (○) treatment in controlled environment studies. The curves represent least squares fits to the UV irradiance (- -) and control treatment (——) elongation rates. The dashed line (-----) represents the expected leaf elongation rate of the UV irradiated leaf if the reduction in elongation rate were solely a function of the depressed photosynthetic rates of that leaf. Each point represents the mean of six replicates. See text for details.

Although UV radiation damage to photosynthesis appeared to accumulate with longer exposure, depression of leaf expansion did not. The reduction of leaf expansion rates was most severe in the very early stages of leaf elongation and apparently involved an effect of UV radiation apart from simply limiting the supply of photosynthate for growth. When daily elongation rates of the first leaf are plotted from initiation of the UV radiation treatment (Fig. 7), it is apparent that leaf expansion rates were depressed below those of the control plant leaf only during the first few days. In this figure is also a plot of the expected expansion rate of the first leaf exposed to UV radiation if growth rates of that leaf were dependent solely on its own photosynthesis for growth and there were no appreciable delay between production of photosynthates and their utilization in the growth process. This hypothetical situation would represent the most pronounced possible case of growth reduction as a consequence of suppressed photosynthetic rates by UV radiation. In this situation, depression of leaf expansion rates would show a cumulative response as did the depression of photosynthesis. Instead, the reduction in expansion rates during the first 2 days of ontogeny suggests that UV irradiation was acting directly on leaf expansion processes. The suppressive effect of UV radiation on expansion rates of subsequent leaves was similar to the first leaf (Fig. 5). In addition, however, the time of leaf exertion was delayed in the plants exposed to UV irradiation. The effects of UV irradiation on development and growth of other leaves later in the treatment may reflect both the direct effects of UV irradiance on leaf expansion processes as well as photosynthate limitation.

The potential of increased solar UV radiation, resulting from partial ozone destruction, to decrease the growth and productivity of sensitive higher plants is apparent in this study. The direct effects of UV irradiance on depressed photosynthetic rates, decreased leaf expansion processes, and also the small stimulation of dark respiration would all contribute to reducing the carbon economy of the plant.

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