Growth and gas exchange in field-grown and greenhouse-grown *Quercus rubra* following three years of exposure to enhanced UV-B radiation

JOHN H. BASSMAN \(^1,3\) AND RONALD ROBBERECHT \(^2\)

\(^1\) Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164–6410, USA
\(^2\) Department of Rangeland Ecology, University of Idaho, Moscow, ID 83844–1135, USA
\(^3\) Corresponding author (bassman@wsu.edu)

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**Summary** Long-term effects of enhanced UV-B radiation were evaluated in field-grown and greenhouse-grown *Quercus rubra* L. (northern red oak), a species with a multiple flushing shoot growth habit. Seeds were germinated and grown in ambient, twice ambient (2×) or three times ambient (3×) biologically effective UV-B radiation from square-wave (greenhouse) or modulated (field) lamp systems for three growing seasons. Greenhouse plants in the 2× treatment had greater heights and diameters during the later part of the first year and into the second year, but by the third year there were no differences among treatments. There were no significant differences in growth among treatments for field plants. Enhanced UV-B radiation did not significantly reduce total biomass or distribution of biomass in either field or greenhouse plants. Net photosynthesis (3×), leaf conductance (2× and 3×) and water-use efficiency (3×) of greenhouse plants were greater in the enhanced UV-B radiation treatments in the second year but unaffected by the treatments in other years. None of the treatments affected these parameters in field plants. Dark respiration was increased by the 3× treatment in the first and third years in greenhouse plants, and by the 2× treatment during the second year in field plants. Enhanced UV-B had variable effects on apparent quantum yield and light compensation points. Chlorophylls were unaffected by enhanced UV-B radiation in both greenhouse and field conditions. Bulk methanol-extractable UV-absorbing compounds were increased only by the 3× treatment in greenhouse plants during the third year and by the 2× treatment in field plants during the second year. Overall, *Q. rubra* appears relatively resistant to potentially damaging enhanced UV-B radiation and is unlikely to be negatively impacted even in the predicted worst-case scenarios.

**Keywords:** biomass, chlorophyll, forest trees, leaf conductance, photosynthesis, ultraviolet radiation, UV-absorbing compounds.

**Introduction**

Enhanced solar ultraviolet-B (UV-B) radiation can cause serious deleterious effects in plants (Lumsden 1997), but the consequences may depend on leaf anatomical properties, shoot growth patterns and canopy architecture (Bassman et al. 2001). Angiosperm leaves are generally considered more susceptible to UV-B radiation than gymnosperm leaves because their spatial distribution of UV-absorbing compounds is less effective at attenuating incoming UV-B radiation (Day et al. 1993). Trees with determinate or multiple flushing shoot growth patterns may be more susceptible to injury than those with indeterminate shoot growth patterns because a particular complement of leaves would be exposed to UV-B radiation for a longer period of time. In indeterminate species, leaves are quickly submerged within the canopy as new leaves are formed at the apex such that any particular leaf experiences constantly attenuating UV-B radiation (Bassman et al. 2001).

Our understanding of the effects of enhanced UV-B radiation on perennial plants, and trees in particular, is limited because relatively few species have been studied. We report here on long-term effects of enhanced UV-B radiation on growth and gas exchange in northern red oak (*Quercus rubra* L.). Northern red oak is a moderate to fast growing angiosperm tree species endemic to the eastern United States north of the southern coastal plain, and Canada in southern Ontario extending eastward to New Brunswick and Nova Scotia (Sander 1990). Northern red oak is intermediate in shade tolerance, and vigorously growing trees typically exhibit a multiple flushing shoot growth pattern (Hanson et al. 1988). It is of substantial ecological and commercial importance and widely planted as an ornamental outside of its native range.

**Material and methods**

**Plant material and growth conditions**

Seeds from open-pollinated *Q. rubra* trees in Pennsylvania were obtained from a commercial nursery. Seeds were stratified (USDA Forest Service 1974) and then sown in 3.0-l pots filled with a standard nursery-potting medium comprising peat and vermiculite. At the time of sowing, the radical of most of
the stratified seed had already emerged. Pots were placed under UV-B lamps and seeds germinated in the respective treatments (see below). Except for the UV-B radiation treatments, radiation, temperature and other environmental variables were ambient. Plants were watered as necessary to maintain soil near field capacity and fertilized at regular intervals with a commercial liquid fertilizer containing N,P,K (20,20,20) and micronutrients. During the winter following the first growing season, plants were transplanted to 6.6-l pots and the second winter to 13.2-l pots. The pots were buried to ground level beneath the lamp frames and mulched to ensure ambient soil temperatures.

For the greenhouse experiment, high-pressure sodium/high intensity discharge lamps (1000 W, HPS/HID) extended the photoperiod to 16 h during the growing season (May through September) and offset shading due to the greenhouse structure. Day/night temperatures in the greenhouse during the growing season were 23/17 °C. Maximum photosynthetically active radiation (PAR; 400–700 nm) at the top of plants ranged from 1800 µmol m–2 s–1 on sunny days to 600 µmol m–2 s–1 on overcast days. To induce dormancy, supplemental lighting and heat were turned off beginning in October of each year and the greenhouse allowed to assume natural photoperiods and near ambient temperatures. Watering and fertilization were also reduced during this time. Normal growing conditions were resumed the following May.

Ultraviolet-B radiation treatments—greenhouse experiment

Supplemental UV-B radiation was supplied over a 10-h period centered on solar noon with Q-Panel UV-B-313 fluorescent lamps (Q-Panel, Cleveland, OH) mounted in metal frames suspended above the pots and filtered with 0.13 mm cellulose diacetate film. For the controls, lamps were filtered with 0.13-mm thick polyester film (absorbs all radiation < 320 nm). Therefore, control plants received only ambient so-

current scenario of projected stratospheric ozone depletion (McKenzie et al. 2003). For each UV-B radiation treatment, four Q-Panel UV-B-313 lamps were mounted at 0.35 m spacing on a 1.25 m x 1.25 m metal frame. Supplemental PAR and UV-A (320–399 nm) were supplied by HPS/HID lamps suspended above the lamp frames. We measured PAR with a Li-Cor 190-SB quantum sensor. Irradiance was 524 kJ m–2 day–1 in the UV-A waveband and 6251 kJ m–2 day–1 (39.5 mol m–2 day–1) in the 400–700-nm waveband (PAR).

Cellulose diacetate filters were changed weekly to minimize spectral changes associated with degradation of the plastic. The filters were exposed to UV-B radiation for 6 h before being applied to the lamps to stabilize their spectral quality. Distance between lamps and plants was adjusted after each filter change to maintain UV-B radiation at target values for each treatment as measured at the mean plant height. For these adjustments, UV-B irradiation was measured with a broadband UV-B sensor (Ultraviolet Meter, Model 3D, Solar Light Co., Philadelphia, PA) calibrated against a spectroradiometer with 0.5-nm discrimination (Optronics 754, Optronics Laboratories, Orlando, FL). Treatments were screened from each other with clear 0.13-mm polyester film (transmittance > 315 nm). To minimize the effects of microenvironmental variation among the treatments, the treatments as well as the plants within treatments were rotated weekly within the greenhouse.

At the end of each growing season, UV-B irradiance was gradually reduced in concert with photoperiod reductions. Ambient treatments were maintained at mean winter values as calculated by the model of Green et al. (1980), modified by Björn and Murphy (1985) (about 1.7 kJ m–2 day–1). In spring, the reverse process was followed. Further attributes of the lamp and filter system, including ratios of UV-B:UV-A:PAR and effects of filter aging on UV-B irradiance, have been described by Bassman et al. (2002) and Warren et al. (2002b).

Ultraviolet-B radiation treatments—field experiment

Field experiments were conducted in an open area adjacent to the greenhouses. Two treatments were examined: ambient UV-BHIE (1x) and two-ambient (2x) UV-BHIE radiation. A modulated, constant addition system (Ashurst Design, Logan, UT), similar to those described by Caldwell et al. (1983), Sullivan et al. (1994a) and Booker et al. (1992), was used to provide enhanced UV-B radiation. The system tracks ambient UV-B radiation and adjusts output of lamps to compensate for solar angle, cloud cover, filter degradation, lamp aging and temperature. Fluorescent lamps (Q-Panel UV-B-313) supplied UV-B radiation. Lamp fixtures were mounted in 1.2 m x 2.4 m metal frames that were adjusted to maintain a constant height above the plant canopies. The long axis of each frame was oriented east—west. Lamp spacing was 35 cm. For the 2x UV-B radiation treatment, lamps were filtered with 0.13-mm thick cellulose diacetate film. For the controls, lamps were filtered with 0.13-mm thick polyester film (absorbs all radiation < 320 nm). Therefore, control plants received only ambient solar UV-B radiation. Filters were replaced at about 3-week intervals. The lamp system was monitored and calibrated at each
Gas exchange determinations

Gas exchange measurements were made in late summer of each year on a set of plants randomly selected from the greenhouse and field studies. Two different systems were employed. The first was an open, compensating gas exchange system (Model BI-7, Bingham Interspace, Logan, UT) connected to an infrared gas analyzer (IRGA; Model 225 MK, Analytical Development, Hoddesdon, U.K.) as described previously (Bassman and Zwier 1991, Bassman et al. 2001). The second system assessed photosynthesis based on $^{14}$C (see below).

Each plant typically produced two flushes of growth during the summer. Using the IRGA system, leaves from each flush were sampled with a portion of the leaf enclosed in a 300 cm$^3$ stainless steel and glass cuvette. Net photosynthesis ($P_n$, mmol CO$_2$ m$^{-2}$ s$^{-1}$), transpiration ($g_t$, mmol H$_2$O m$^{-2}$ s$^{-1}$) and stomatal conductance ($g_s$, mmol H$_2$O m$^{-2}$ s$^{-1}$) were determined at leaf temperatures of 25 °C and minimal leaf-to-air vapor density differences (VDD usually ≤ 5.0 g m$^{-3}$). Responses to PAR were made at intervals of 30 mmol m$^{-2}$ s$^{-1}$ from 0 to 150 mmol m$^{-2}$ s$^{-1}$ and at 100 mmol m$^{-2}$ s$^{-1}$ intervals from 200 through 1000 mmol m$^{-2}$ s$^{-1}$. A 1000 W HPS/HID lamp was used to supply different irradiances of PAR by varying lamp height above the cuvette. Carbon dioxide exchange rates in the dark were used as a measure of dark respiration ($R_d$, mmol CO$_2$ m$^{-2}$ s$^{-1}$). Regressions of irradiance and net carbon dioxide exchange over the range of 0 to 200 mmol m$^{-2}$ s$^{-1}$ PAR were used to determine light compensation points (LCP, mmol m$^{-2}$ s$^{-1}$) and quantum yield ($\Phi$, mmol CO$_2$ mol$^{-1}$ photons). Quantum yield was calculated as the slope, and LCP as the x-intercept of these regressions (Björkman 1981, Long and Hällgren 1987). Light response curves were generated by plotting $P_n$ as a function of PAR. These curves were fitted to a model of the form:

$$P_n = P_{\text{max}}(1 - e^{-\Phi \text{PAR}}) - R_d$$

where $P_{\text{max}}$ = maximum rate of photosynthesis and other terms are as previously defined (Landsberg 1977). All other gas exchange parameters were determined as described in Bassman and Zwier (1991). Net photosynthesis was light saturated at PAR ≥ 600 mmol m$^{-2}$ s$^{-1}$. Consequently, gas exchange variables averaged for PAR ≥ 600 mmol m$^{-2}$ s$^{-1}$ were used to compare treatment effects at saturating or near saturating irradiances. Following gas exchange measurements, leaf area enclosed in the cuvette was measured with a leaf area meter (Delta-T Devices, Cambridge, U.K.) and photosynthesis expressed on an area basis.

During the third year of the field study, in situ measurements of photosynthesis were made on field plants with a portable $^{14}$CO$_2$ gassing device, slightly modified in design from those described by Michael et al. (1985) and McWilliam et al. (1973). Details of the method and calculations have been described by Michael et al. (1985). Measurements of $^{14}$C-photosynthesis were made during clear midday periods with plants removed from under the lamp frames. Concurrent measurements of PAR, leaf temperature and atmospheric humidity were made at the time of $^{14}$C exposure. A portion of the leaf midway between the tip and base was clamped between the upper and lower treatment chambers. The cuvette was tilted at an angle normal to the sun and air containing 350 cm$^3$ m$^{-3}$ CO$_2$ (specific activity 216.7 MBq m$^{-3}$ $^{14}$CO$_2$) was passed through the chamber (flow rate = 1.33 cm$^3$ s$^{-1}$) and over both surfaces of the leaf for 30 s. Immediately following exposure, a 0.528 cm$^2$ section was cut from the exposed portion of each leaf with a cork borer. Each section was immediately placed in a scintillation vial containing 1.5 cm$^3$ BTS tissue solubilizer (Beckman Instruments, Fullerton, CA) and taken to the laboratory for assay of radioactivity. To remove color, 0.5 ml of H$_2$O$_2$ was added to each vial and the leaf segments digested for 24 h at 50 °C. After cooling for at least 30 min, three drops of glacial acetic acid and 17 ml of ScintiVerse II (Fisher Scientific, Fair Lawn, NJ) liquid scintillation cocktail were added to each vial. Following an additional 24-h dark equilibration period, radioactivity of the samples was determined with a Packard 1900CA liquid scintillation spectrometer (Packard Instrument Co., Meriden, CT). The rate of photosynthesis, based on sample dpm, was calculated as described by Michael et al. (1985). Values determined by this technique closely compared with those obtained by IRGA methods, but tend to be about 5% higher. They are considered an approximation of gross ($P_g$) rather than net ($P_n$) photosynthesis (Michael et al. 1985) and are termed apparent photosynthesis ($P_A$).

Growth and biomass distribution

Total height and diameter were measured weekly or bi-weekly on all plants during each growing season. During late summer of each year, a subsample of plants from both the greenhouse and field studies was harvested for intermediate growth and biomass determinations. Final harvests were conducted at the end of the third growing season. Heights, diameters and distribution of biomass within plants were determined immediately following gas exchange measurements. Plants were partitioned into leaves (main stem leaves, lateral branch leaves), stem (main stem and lateral branches) and roots. Each biomass component was further partitioned into within- and between-year growth fluxes. Before drying, leaf area for each foliage component was determined with a leaf area meter. Biomass components were dried separately at 70 °C to constant mass and weighed. Shoot to root ratios (mass basis) were calculated for each plant.
**Pigment analysis**

At harvest, two samples from each flush (1.0 cm² each) of leaves on each plant were excised. One sample was placed in a light-proof scintillation vial containing 5.0 ml N,N-dimethylformamide (DMF) and stored in the dark for 24 h at 4 °C. Total chlorophyll, chlorophyll a and chlorophyll b were determined after extraction as described by Inskeep and Bloom (1985).

The second sample was placed in a 20-ml test tube for determination of methanol-extractable UV-absorbing compounds. Samples were dried at 95 °C for at least 24 h, then ground in a tissue homogenizer in 10 ml of methanol:H₂O:HCl (70:29:1, v/v). The extract was centrifuged at 600 g for 10 min and absorbance of the supernatant determined spectrophotometrically at 290, 300 and 310 nm. Relative absorbance, calculated on a leaf area basis, was used as an index of UV-absorbing compounds (Robberecht and Caldwell 1986).

**Experimental design and data analysis**

For the greenhouse study, variation in germination resulted in establishment of between 47 and 49 plants per treatment. In the field, 93 to 95 seedlings germinated. Individual plants were treated as independent replicates within treatments. The number of single-plant replications available for weekly measurements in each treatment varied depending on survival and previous harvesting. Four to 12 plants were selected from each treatment each year for gas exchange and harvest. Plants selected were based on uniformity in size and appearance. Exterior border trees were excluded. Data were treated as a completely randomized design and subjected to one-way analysis of variance (ANOVA) or regression analysis (GLM procedure) using the SAS statistical package (SAS Institute, Cary, NC). Where appropriate, error terms were partitioned with a nested ANOVA model (e.g., plants within treatment, leaves within plants, etc.). Individual means were compared with Duncan’s Multiple Range Test and differences were considered significant at \( P \leq 0.05 \). For details of the study design see Bassman et al. (2002).

**Results**

**Growth**

During the first year of the greenhouse experiments, height growth of trees in the 2× treatment lagged behind that in the ambient UV-B radiation and 3× treatments during the first flush, but exceeded height growth of trees in these treatments during the second flush (Figure 1). Consequently, trees in the 2× treatment were significantly taller than trees in the ambient and 3× treatments at the end of the first year (Figure 1). Trees in the 2× treatment began the second year taller than trees in the ambient and 3× treatments, but grew little during the second flush that year. By Year 2, there were no significant treatment differences in height growth, a trend that continued throughout Year 3 (Figure 1). In the field experiments, patterns of height growth were similar for trees in the ambient and 2× treatments throughout all three years (Figure 1). Patterns in diameter growth mirrored patterns in height growth in both the greenhouse and field studies.

**Biomass distribution**

In the greenhouse study, trees in the 2× treatment produced less leaf area and biomass on lateral branches than trees in ambient UV-B radiation. This contributed to a lower total leaf biomass in 2× trees compared with trees in ambient UV-B radiation (\( P = 0.102 \) second year; \( P = 0.125 \) third year; Figure 2). Leaf biomass on lateral branches was also less for trees in the 3× treatment during the second year (\( P = 0.077 \), but not in the...
third year; total leaf biomass was similar for 3× trees and those in ambient UV-B radiation (Figure 2).

Lateral stem biomass was reduced on 2× trees compared with trees in ambient UV-B radiation during the second and third year of the greenhouse study, but this resulted in no significant reduction in total stem biomass (Figure 2). The 3× treatment had no effect on stem biomass (Figure 2). The 2× treatment slightly reduced aboveground biomass in Years 2 and 3 ($P = 0.131$), whereas the 3× treatment had no effect on aboveground biomass. Root biomass was significantly reduced by both 2× and 3× treatments during the first year, but not during Years 2 and 3 (Figure 2). Total plant biomass did not differ significantly among treatments during any year of the greenhouse study (Figure 2) although shoot:root ratios were reduced in the 2× plants in Years 1 and 2.

In the field study, lateral leaves ($P = 0.058$), lateral stem ($P = 0.107$) and lateral leaf area ($P = 0.062$) were all reduced by the 2× treatment during the first year, but not in subsequent years. Otherwise, enhanced UV-B radiation had no effect on biomass production and distribution (Figure 2).

**Gas exchange**

In the greenhouse study, rates of $P_n$ at saturating irradiances were higher in 3× trees than in ambient and 2× trees during the first ($P = 0.0931$) and second ($P < 0.05$) years, but not the third year (Figure 3). Compared with ambient and 2× trees, dark $R_d$ were also significantly higher in 3× trees during Years 1 and 3, but not in Year 2 (Figure 3). There were no significant treatment effects on $K$ during the three years of study, but $g_s$ was significantly higher in 2× and 3× trees than in trees in the ambient UV-B regime during Year 2 (Figure 3). Compared with trees in ambient UV-B radiation, water-use efficiency (WUE) was higher in both 2× (not significant) and 3× trees during Year 1 and in 3× trees during the Year 2; however, there were no significant differences during Year 3 (Figure 3). Leaf inter-
nal CO₂ concentrations (Cᵢ) were greater for 2× trees and less for 3× trees compared with trees in ambient UV-B radiation during Year 2. Otherwise there were no significant differences in Cᵢ among the treatments (data not shown). In the field study, R₉ was greater in 2× trees for first flush leaves during Year 2, otherwise there were no significant treatment differences in any gas exchange variables for first flush leaves (Figure 3).

Detailed responses of photosynthesis to irradiance were evaluated in greenhouse-grown trees during the first year of the study and are reported in Bassman et al. (2003). Enhanced UV-B radiation had no effect on the shape of the light response curve. Apparent quantum yields were reduced in 3× trees compared with ambient and 2× trees during Year 1 (Table 1). During Year 2, Φ was lower in 2× trees than in ambient and 3× plants; however, there were no differences between treatments during Year 3 (Table 1). Light compensation points were less for 2× trees than for ambient and 3× trees during Years 2 and 3. During Year 3, LCPs increased with increasing UV-B irradiance (Table 1). In the field study, there were no significant treatment differences in Φ or LCP in Year 1. Apparent quantum yields were similar, but LCPs were higher in 2× trees during Year 2 (Table 1).

Leaf pigments

In the greenhouse study, chlorophylls a and b and total chlorophyll were generally higher in 2× and 3× trees than in trees in ambient UV-B radiation during Year 1. In Year 2, chlorophyll in first flush leaves was unaffected by the treatments, but was increased by the 3× treatment in second flush leaves. No differences were detected during Year 3. Ratios of chlorophyll a:chlorophyll b in greenhouse plants were unaffected by the treatments in all years. In the field study, chlorophyll concentrations were similar in ambient and 2× trees in all study years (data not shown).

Methanol-extractable UV-absorbing compounds (A₃₅₀) in greenhouse trees were similar between treatments during Year 1 (Figure 4). There were no significant differences within either flush during Year 2. However, when both flushes were combined, 2× trees had lower amounts of UV-absorbing compounds than either ambient or 3× trees. In Year 3, UV-absorb-
ing compounds in first flush leaves were higher in 3× trees than in ambient and 2× trees (Figure 4); there were no treatment differences in UV-absorbing compounds in second flush leaves or when both flushes were combined.

In the field study, amounts of UV-absorbing compounds were similar among treatments during Year 1, but 2× trees had higher amounts of UV-absorbing compounds in first flush leaves during Year 2 (Figure 4). There were no significant differences between treatments in second flush leaves, but when both flushes were combined, UV-absorbing compounds were significantly greater in 2× trees than in ambient trees (not shown). No significant differences in UV-absorbing compounds between treatments were observed during Year 3.

**Discussion**

The study trees typically produced two and occasionally three flushes of growth during a growing season. Consequently, each flush of leaves was exposed to higher doses of UV-B radiation for a longer period of time than for the leaves of an equivalent indeterminate angiosperm species such as *Populus trichocarpa* Torr. & A. Gray, which we evaluated by similar protocols (Bassman et al. 2001). Nevertheless, enhanced UV-B radiation was generally not deleterious to the growth and physiology of *Q. rubra*, even when supplied at high rates and for a long time.

In part, the resistance of *Q. rubra* to UV-B may be associated with the high constitutive amounts of UV-absorbing compounds in leaves. Although we observed some stimulation of methanol-extractable UV-absorbing compounds in the greenhouse and field studies, in many cases enhanced UV-B radiation had no effect on these compounds. Oaks have high concentrations of phenylpropanoids that are probably effective anti-herbivore compounds (Feeny 1969, 1970). Previously, we found that total flavonoid concentration in *Q. rubra* was more than twice that of the other tree species evaluated, with the predominant compound nearly 20 times (by mass) that of any eluted compound from any of the other species (Warren et al. 2002b). Enhanced UV-B radiation also resulted in a change in flavonoid composition, with fewer early eluting compounds and more late eluting compounds (Warren et al. 2002b).

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**Table 1. Effects of UV-B radiation on apparent quantum yield (Φ, µmol CO₂ µmol⁻¹ photons) and light compensation point (LCP, µmol photons m⁻² s⁻¹) in *Quercus rubra* seedlings (n = 28 per treatment). Values followed by different letters in the same column for the same experimental conditions (greenhouse or field) are significantly different (P ≤ 0.05). Abbreviation: N.A. = not measured.**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Quantum yield (Φ)</th>
<th>Light compensation point (LCP)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Year 1</td>
<td>Year 2</td>
</tr>
<tr>
<td><strong>Greenhouse</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambient</td>
<td>0.0335 a</td>
<td>0.0211 a</td>
</tr>
<tr>
<td>2× Ambient</td>
<td>0.0334 a</td>
<td>0.0135 b</td>
</tr>
<tr>
<td>3× Ambient</td>
<td>0.0279 b</td>
<td>0.0241 a</td>
</tr>
<tr>
<td><strong>Field</strong></td>
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</tr>
<tr>
<td>Ambient</td>
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<td>0.0345 a</td>
</tr>
<tr>
<td>2× Ambient</td>
<td>0.0346 a</td>
<td>0.0358 a</td>
</tr>
</tbody>
</table>

**Figure 4.** Relative absorbance of methanol extracts at 300 nm (A₃ₐ₀; UV-absorbing compounds) in *Quercus rubra* seedlings subjected to ambient, 2× ambient or 3× ambient UV-B radiation for Pullman, WA. Values are means from first flush leaves of 4–14 replicate trees (n) per treatment ± 1 SE of the mean (vertical lines). Bars with different letters for the same condition (field or greenhouse) and year are significantly different (P ≤ 0.05) according to Duncan’s Multiple Range Test.
Enhanced UV-B radiation can also affect plant morphology, which in turn affects penetration of UV radiation to sensitive tissue. Antonelli et al. (1998) reported that enhanced UV-B radiation increases leaf thickness and accumulation of phenolic compounds in cell walls of adaxial epidermis tissue of Quercus robur L. Oak leaves produce abundant surface trichomes (Karabourniotis et al. 1992) which contain considerable quantities of phenolics (Karabourniotis et al. 1998, Skaltsa et al. 1994) and significantly attenuate UV-B radiation even before it encounters the leaf epidermis (Karabourniotis and Bornman 1999, Karabourniotis et al. 1992, Skaltsa et al. 1994). Enhanced UV-B radiation can stimulate trichome production in Q. rubra seedlings (Nagel et al. 1998). Trichome density varies with radiation environment in Quercus coccifera L. and Quercus ilex L. (Liakoura et al. 1997) and shade leaves have lower amounts of UV-absorbing compounds than sun leaves (Filella and Penuelas 1999, Liakoura et al. 2003). Whatever the specific changes in UV-absorbing compounds, Q. rubra appears well protected against the adverse effects of enhanced UV-B radiation.

In many species, enhanced UV-B radiation reduces growth, often accompanied by reduced leaf area and changes in carbon allocation and partitioning (Bassman 2004, Caldwell et al. 2003). However, growth and biomass may also be increased in response to enhanced UV-B radiation (Caldwell et al. 2003). Our results are consistent with several studies on angiosperm tree species that show minimal effects of enhanced UV-B radiation on growth and biomass allocation. For example, Sullivan et al. (1994b) found that biomass of Liquidambar styraciflua L. seedlings was unaffected by supplemental UV-B radiation applied for two years in field conditions. However, these seedlings exhibited subtle changes in carbon allocation and growth. Final leaf size was unaffected, but rates of leaf elongation and accumulation of leaf area were lower in leaves exposed to enhanced UV-B radiation (Dillenburg et al. 1995). DeLucia et al. (1994) reported that supplemental UV-B radiation had no effect on growth of Amelanchier arborea (Michx. f.) Fern., Betula papyrifera Marsh., Nyssa sylvatica Marsh. and Robinia pseudoacacia L. Total biomass, plant height and leaf area were significantly reduced in Cercis canadensis L. and Morus alba L. However, there was no clear demarcation of response based on the shade tolerance of the species evaluated. Cybulski and Peterjohn (1999) reported no effects on aboveground biomass in Q. rubra subjected to zero or ambient UV-B radiation. Enhanced UV-B radiation decreased growth rates and leaf area in Betula pubescens J. F. Ehrh. in greenhouse conditions, but not in the field (Weih et al. 1998). In P. pendula enhanced UV-B reduced height and diameter beginning in the third year, whereas biomass and other parameters remained unchanged (Tegelberg et al. 2001).

Values for most of the gas exchange variables that we observed were in the range reported by other studies of oaks for $P_a$ (Hanson et al. 1988, Weber and Gates 1990, McGraw et al. 1990, Kruger and Reich 1993a, 1993b, g, (Kubiske and Abrams 1992, Kruger and Reich 1993a, Hanson et al. 1994) and $R_g$ (Heichel and Turner 1983, Hanson et al. 1988, McGraw et al. 1990), but our WUE values were higher (Ni and Pallardy 1991). Enhanced UV-B radiation either had no effect or slightly increased $P_a$ (Figure 2). In Quercus gambelii Nutt., enhanced UV-B radiation increased photosynthesis on a leaf area basis, but not on a leaf mass basis (Harley et al. 1996). In Q. robur, enhanced UV-B radiation had no effects on photosynthesis (Antonelli et al. 1998), but in many other species photosynthesis is reduced by enhanced UV-B radiation, usually in conditions of high ratios of UV-B:PAR (Fiscus and Booker 1995). However, Bassman et al. (2001) observed stimulation of photosynthesis by enhanced UV-B radiation in Populus deltoides Bartr. ex Marsh and similar effects have also been recorded for Acer rubrum L., Liquidambar styraciflua (Sullivan et al. 2003) and Picea engelmannii Parry ex Engelm. (Bassman et al. 2003), but not in Liriodendron tulipifera L. (Sullivan et al. 2003), Populus trichocarpa (Bassman et al. 2003) or Pseudotsuga menziesii (Mirb.) Franco (Bassman et al. 2002). Sullivan et al. (2003) suggested that photosynthetic enhancement by UV-B radiation in Acer rubrum could be due to enhanced blue light absorption or fluorescence induced by UV-B radiation absorbance by hydroxycinnamates (HCAs). Although we did not assay these compounds in the present study, phenolic profiles observed in earlier studies on Q. rubra imply that HCAs could play a role in this species (Warren et al. 2002b). The high concentration of leaf phenolics likely prevented damage to the photosynthetic apparatus.

Effects on photochemistry associated with photosynthesis were inconclusive. In contrast to other angiosperms (Bassman et al. 2003, Sullivan et al. 2003) and some gymnosperms (Bassman et al. 2003), enhanced UV-B radiation had no significant effect on the shape of the light response curve. Greenhouse-grown plants sometimes displayed a depression in $\Phi$ in enhanced UV-B radiation (see Table 1); however, no such effects were seen in field-grown plants. Light compensation points were reduced in some cases, but increased in others. In total, the data suggest no significant impact of UV-B radiation on the photosynthetic apparatus, which is consistent with conclusions reached by Sullivan et al. (2003) for some other angiosperm tree species. Bassman et al. (2003) found that changes in $\Phi$ and LCPs accompanied changes in $P_a$ associated with enhanced UV-B radiation in three of five tree species (Bassman et al. 2003). In other tree species, $\Phi$ was unaffected (Naidu et al. 1993, Dillenburg et al. 1995) or significantly reduced (Sullivan and Teramura 1989) by enhanced UV-B radiation and negative effects on photochemistry have been reported for Picea abies L. grown in a greenhouse (Baycon et al. 1996, Pukacki and Modrzynski 1998). Bassman et al. (2002) observed increases in both $\Phi$ and LCPs in Pseudotsuga menziesii in enhanced UV-B radiation.

Enhanced UV-B radiation either had no significant effect or increased dark respiration rates in both greenhouse and field plants. Increased $R_d$ may be related to higher metabolic rates associated with conversion of carbon to secondary compounds because they corresponded to those cases where UV-absorbing compounds also increased (see Figures 2 and 4). Enhanced UV-B radiation did not affect $R_d$ in a range of crop plants (Teramura et al. 1980, Marke and Tevini 1996, Hunt and McNeil 1998), but small increases were seen in Rumex pat-

Slight increases in $P_a$ relative to $K$ in the first two years accounted for the improved instantaneous WUE observed for greenhouse plants grown in enhanced UV-B radiation (see Figure 2). Although UV-B radiation may have direct effects on $g_s$ (Allen et al. 1998, Nogués et al. 1998), the observed changes in WUE were probably insufficient to substantially affect changes in drought resistance as observed for some Mediterranean pines (Petrovoulou et al. 1995) and pea plants (Nogués et al. 1998). Keiller and Holmes (2001) suggested that changes in WUE were a significant factor in plant response to UV-B radiation. In greenhouse conditions, enhanced UV-B radiation resulted in higher WUEs in *Pinus ponderosa* Doug. ex P. Laws & C. Laws (Bassman et al. 2003) and *Populus deltoides* (Bassman et al. 2001), but reduced WUEs in *Populus trichocarpa* (Bassman et al. 2003). Under field conditions, WUEs increased in *Acer rubrum* and *Liriodendron tulipifera*, but not in *Liquidambar styraciflua* (Sullivan et al. 2003).

The use of constant, day-long UV-B irradiation, as employed in our greenhouse study, usually produce higher daily and seasonal UV radiation doses because there is no compensation for changing solar angles or deviations from clear sky conditions (see Sullivan et al. 1994a, Bassman et al. 2002). However, even though our greenhouse plants probably received higher annual doses than the treatments suggest, midday irradiance environments were similar between greenhouse and field experiments (Bassman et al. 2002). Nevertheless, the lamps used to supply both UV-B radiation and PAR may have confounded the results. As the filters aged, UV-B radiation may have been reduced by 40% or more between changes for the greenhouse lamp system (Warren et al. 2002a). Consequently, the mean dose supplied to plants was less than the normal dose. Because lamp outputs were less in the field, filter aging imposed less than a 10% reduction in UV-B irradiance between filter changes (Warren et al. 2003). The UV-B 313 lamps emit considerable quantities of radiation in the UV-A and blue light wave bands, possibly sufficient to drive low irradiance blue light responses (including photorepair) (Jolley et al. 1987, Adamse et al. 1994, Sullivan et al. 2003, Krizek 2004) and the lack of response in growth and chlorophyll data suggest this might be the case. These would likely have been greater in the greenhouse study because of the closer proximity of plants to lamps in the higher UV-B irradiance treatments. Still, most of the significant effects we observed occurred in the greenhouse study and at the higher UV-B irradiances, consistent with the long-standing observation that effects of UV-B radiation are exaggerated in greenhouse experiments (Caldwell et al. 2003). This is in contrast to our results for *Pseudotsuga menziesii* in which the direction and magnitude of changes were similar between greenhouse and field plants (Bassman et al. 2002).

Despite UV-B irradiation regimes that resulted in doses much higher than might be expected in the worst-case environment change scenarios, long-term exposure to enhanced UV-B radiation had little effect on photosynthesis and growth in northern red oak, which has a determinate (multiple flushing) shoot growth pattern. Leaves of *Q. rubra* possess large quantities of phenolic compounds combined with surface trichomes that effectively limit the penetration of UV-B radiation, thus minimizing its potential adverse effects. However, other processes (e.g., effective photorepair) may also contribute resistance to enhanced UV-B radiation. Based on three years of data from greenhouse and field experiments, we conclude that even substantial increases in UV-B radiation are unlikely to have cumulative, deleterious effects on the growth of *Q. rubra*.

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**References**


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Populus trichocarpa, Quercus rubra, Pseudotsuga menziesii, and Pinus ponderosa exposed to enhanced ultraviolet-B radiation. Physiol. Plant. 65:483–488.


