



Effects of ambient UV-B radiation on the above-ground biomass of seven temperate-zone plant species

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Abstract

Variations in the amount of solar ultraviolet-B radiation (UV-B) reaching the biosphere may alter productivity in non-agricultural plants. We examined how ambient levels of UV-B modify the biomass of seven temperate-zone species including three grass species (*Echinochloa crusgalli*, *Setaria faberi*, *Elymus virginicus*), three forbs (*Verbascum blattaria*, *Lactuca biennis*, *Oenothera parviflora*), and one tree species (*Quercus rubra*). Plants were grown outside in enclosures near Morgantown, WV, USA (39° N, 79° W) for one season under near-ambient or no UV-B conditions. The different levels of UV-B were achieved using filters which differentially transmit UV-B irradiance. There was a trend towards reduced above-ground biomass in *L. biennis* (14%) and significantly increased above-ground biomass in *O. parviflora* (10.2%) under ambient UV-B. The partitioning of biomass between individual plant parts was altered by ambient UV-B in *O. parviflora*. Leaf biomass was significantly increased (18%), and there were trends toward increased stem (6.7%) and reproductive (9%) biomass. In addition to biomass stimulations, *O. parviflora* grew significantly taller (5.3%) under ambient UV-B. This study provides evidence that some non-agricultural plants exhibit species-specific growth responses to variable UV-B, with short-lived forbs appearing to be the most sensitive. If the biomass and morphological alterations observed for the forbs in this study were to persist over several years, they might modify population dynamics, competitive interactions, and productivity in ecosystems as UV-B levels fluctuate in the future.

Introduction

Reductions in stratospheric ozone of approximately 10–11% have occurred in northern midlatitudes from 1979–1993 due to anthropogenic pollution (Callis et al. 1997; Bojkov & Fioletov 1997). This decrease in the thickness of the stratospheric ozone layer has led to increases of nearly 10% in the amount of solar UV-B radiation (UV-B) reaching the earth's surface at several midlatitude locations (Herman et al. 1996; Kane 1998). Changes in the amount of UV-B reaching the biosphere could have substantial negative or positive impacts on plant productivity (Caldwell et al. 1995; Rozema et al. 1997b). Most plants that are responsive to UV-B have reduced biomass under higher UV-B levels (Bogenreider & Klein, 1982; DeLucia et al. 1994; Searles et al. 1995; Sullivan et al. 1994; Tosserams et al. 1997). However, a small number of

species exhibit stimulations in growth under higher UV-B (Barnes et al. 1990; Musil 1995; Musil & Wand 1994; Tosserams et al. 1997).

Traditionally, photobiologists use two methods for assessing plant sensitivity to variations in UV-B radiation – supplementation studies or exclusion studies (Caldwell & Flint 1994). Supplementation studies use lampbanks of fluorescent lights to supplement ambient levels of UV-B and have the advantage of directly assessing if elevated levels of UV-B will affect plant physiology and development. A drawback, however, is that lamp systems can be costly, require a source of electrical power, and can be difficult to operate and maintain, in remote locations. Exclusion studies use plastic films with different UV-B transmission properties to filter natural sunlight and have several advantages over lampbank systems. First, the use of films is less expensive than lampbanks, especially

modulated lamp systems. A second advantage is that exclusion studies require minimal maintenance and no power source; this makes them ideal for field studies, especially in remote locations. A final advantage is that exclusion eliminates some confounding effects that occur in elevated studies which make their results difficult to interpret and compare. For example, lampbanks deliver supplemental UV-A along with UV-B, and special care must be taken to isolate UV-B effects (Newsham et al. 1996). In contrast, films used in exclusion studies have little effect on UV-A while strongly attenuating levels of UV-B.

Along with the practical advantages of exclusion studies, their ultimate value is that they appear to effectively identify plants with the greatest sensitivity to elevations in UV-B (Caldwell & Flint 1994). Evidence for this claim comes from situations where the same species have been examined using both experimental methods. For example, the species *Calamagrostis epigeios*, *Plantago lanceolata*, and *Verbascum thaspus* were determined to be unresponsive in biomass parameters under both exclusion (ambient vs no UV-B) and lampbank (ambient vs elevated UV-B) studies (Tosserams et al. 1996, 1997). In addition, *Vigna radiata* (cv. PS-16) had reduced biomass under higher UV-B treatments in experiments using both methods (Pal et al. 1997; Singh 1997; Singh & Agrawal 1996). Two other useful observations can be made by comparing methods. One is that in the studies examined, the magnitude of the change in mean biomass was always larger when lampbanks were used – this was true whether the lampbanks were used under greenhouse or field conditions. For example, the total above-ground biomass in *Vigna radiata* was only lowered 29.8% under ambient UV-B in an exclusion study (Pal et al. 1997) but was reduced by 49–64% under elevated UV-B in lampbank studies conducted under field conditions (Singh 1997; Singh & Agrawal 1996). The second observation is that the pattern of UV-B effects on mean biomass were consistent between methods; *V. radiata*, *P. lanceolata*, and *V. thaspus* had reduced biomass and *C. epigeios* had increased biomass under higher UV-B levels using either method (Pal et al. 1997; Singh 1997; Singh & Agrawal 1996; Tosserams et al. 1996, 1997). Therefore, exclusion studies seem to identify the most sensitive species and can indicate the general pattern of response for these species to elevated UV-B levels.

In this study, we used the exclusion method to examine the responsiveness to variations in UV-B of seven non-agricultural, temperate-zone plant species

from different life forms. Natural species were chosen because our current understanding of UV-B effects is biased toward agricultural species (Rozema et al. 1997a; Teramura 1990). Only a limited number of studies have examined the effects of UV-B on plants from natural ecosystems compared to agricultural plants (McLeod & Newsham 1997; Rozema et al. 1997a), despite the fact that crops account for only 6% of productivity worldwide (Vitousek et al. 1986).

The goal of our study was to examine if variable levels of natural UV-B would affect above-ground biomass production in plant species that normally reside in field and forest ecosystems of the Eastern United States. We examined the UV-B sensitivity of seven species including three grasses (*Echinochloa crusgalli*, *Setaria faberi*, *Elymus virginicus*), three forbs (*Verbascum blattaria*, *Lactuca biennis*, *Oenothera parviflora*) and one tree (*Quercus rubra*) by growing them under natural levels of UV-B or in the absence of ambient UV-B.

Methods

Six experimental enclosures were located in an open area at the West Virginia University Horticultural Farm (elevation 397 m) near Morgantown, WV USA (39° N, 79° W). Three replicate enclosures were used for each of the two UV-B treatments: ambient and no UV-B. Each enclosure consisted of a wooden frame (1.53-m-wide × 1.53-m-deep × 1.83-m-tall) with a pitched roof. The roof and all sides of each chamber were covered with either 0.13-mm thick polyester plastic film (optically equivalent to Mylar-D, Dupont, Wilmington, DE) for no UV-B treatments or 0.038-mm thick Teflon film (Type 300 A, Dupont, Wilmington, DE) to provide the near ambient UV-B treatments. Although both films are highly transparent (>90%) to PAR, they differ in their transparency to UV-B – polyester film has a steep transmission cut-off at 320 nm, whereas Teflon transmits 85% of radiation in the UV-B range (Figure 1). Temperatures both inside and outside each enclosure were monitored daily using max/min thermometers. The average daily temperature at our study site ranged from 14.7 to 27.1 °C during the growing period from June to mid-October, 1996. The temperatures inside the enclosures never differed more than 1.2 °C from the external air temperature.

Biologically effective UV-B weighted to 300 nm using the generalized plant action spectrum of Caldwell (1971) was measured monthly both inside and

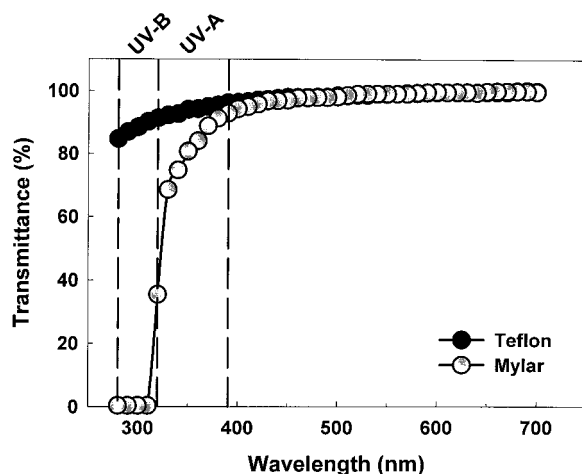


Figure 1. Transmission spectra for polyester and Teflon films determined using a UV-visible recording spectrophotometer.

outside of the enclosure frames. These measurements were made during clear-sky conditions using a Skye Instruments UV-B sensor that had been calibrated with a double-monochromator UV-visible spectroradiometer (model 742, Optronic, Orlando, FL). The highest biologically effective UV-B outside the enclosures was $8.1 \text{ kJ m}^{-2} \text{ d}^{-1}$ recorded in mid-July. The lowest biologically effective UV-B was $1.8 \text{ kJ m}^{-2} \text{ d}^{-1}$ recorded immediately prior to harvest in October. On average, the biologically effective UV-B under the Teflon-covered enclosures was 88–90% of ambient levels, while UV-B measured under the polyester-covered frames was $\leq 4\%$ of ambient levels. The PAR under the plastic filters was 91.3% of ambient for Teflon and 88.6% of ambient for polyester as measured with a quantum sensor (LiCor, Lincoln, NE). Filters were replaced monthly, and only minimal photodegradation occurred for the Mylar filters and none for the Teflon filters during the 30-day time period. The extent of photodegradation was determined in the laboratory by measuring the transmittance spectra of aged films using a UV-visible recording spectrophotometer (model UV160U, Shimadzu Scientific Instruments, Columbia, MD).

A total of 180 plants of each species (1260 plants total) were grown under the two UV-B treatments. The seeds for each species were collected locally from wild plants and planted in 15×30 -cm cylindrical pots within the enclosures. Upon germination, seedlings were thinned to a density of three plants per pot. Multiple plants were grown per pot to obtain adequate plant material for a separate study of UV-B effects on

litter chemistry and decay. All pots were filled with Pro-mix BX potting soil. The pots were watered to saturation each morning and afternoon during the growth period. During weekday mornings, pots were also fertilized with 200-mL of half-strength Hoagland's solution (10.2 mM N, 3.1 mM K, 2.6 mM Ca, 1.0 mM P, 1.0 mM Mg, 1.0 mM S, 0.08 mM Cl, 0.05 mM Fe, 0.02 mM B, $2.0 \mu\text{M}$ Zn, $2.0 \mu\text{M}$ Mn, $0.1 \mu\text{M}$ Cu, $0.09 \mu\text{M}$ Mo). Pots rested on platforms 0.75 m above the ground under each enclosure; thus, the only nutrients and water received by each replicate were those we applied to the individual pots.

The experimental set-up was a complete block design with nesting. It consisted of three replicate enclosures per UV-B treatment level, with 10 pots of each species randomly assigned to and positioned under each replicate enclosure. Therefore, pots were the replicated unit within treatment enclosures, and the response variables to estimate treatment effects were measured on a per pot basis. Since there were three enclosures per UV-B level, there were a total of 30 replicate pots for each treatment-species combination. Enclosures were arranged in a straight line due to the topography of the study site. Treatments were assigned to enclosures in a systematic pattern in accordance with the recommendations of Hurlbert (1984) to avoid position effects that could arise from a purely random placement. During the experiment, the pots were randomly rotated under each frame to eliminate position effects within enclosures on individual pots. At the end of the growing season, fertilization was terminated, and all above-ground tissue from each pot was collected, dried for 48 h at 65°C , and weighed.

Further examination of UV-B growth effects was performed for two species, *Q. rubra* and *O. parviflora*, to see how UV-B altered biomass partitioning between individual above-ground plant parts. We measured partitioning between *Q. rubra* stem and leaf biomass, and *O. parviflora* stem, leaf, and seed pod biomass. In addition, we measured the total height and number of seed pods for *O. parviflora* immediately before harvest. We chose these two species for a more detailed growth analysis because *Q. rubra* is an economically important tree species, and *O. parviflora* showed interesting growth responses to variable UV-B during treatment.

UV-B induced changes in total above-ground biomass for all species and in individual biomass and growth parameters for *Oenothera* and *Quercus* species were analyzed using separate nested one-way analysis of variance (ANOVA) tests. The main effects in the

Table 1. Statistical design determining the effects of UV-B on the total above-ground biomass or individual biomass components and growth parameters of each plant species.

Effects in model	df	E (MS)	Den (MS)	Effect
Treatment	1	$\sigma^2 + \sigma_{E[T]}^2 + K_T^2$	Enc. (treat.)	Fixed
Enclosure (treat.)	4	$\sigma^2 + \sigma_{E[T]}^2$	Error	Random
Error	54	σ^2		
C Total	59			

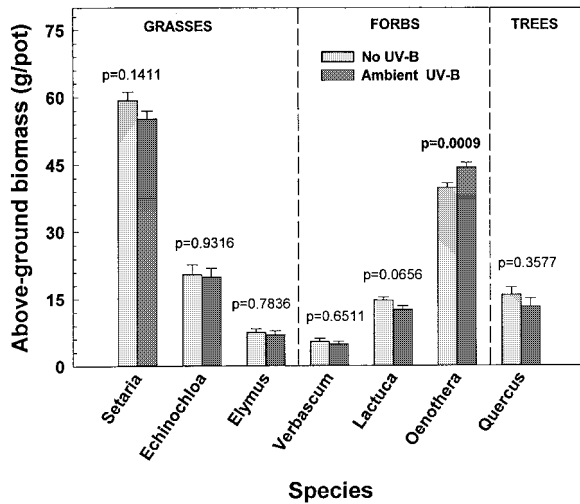


Figure 2. Above-ground biomass of three grasses, three forbs, and one tree grown under no and ambient UV-B. Bars represent one standard error of the mean. P values in bold type indicate a significant UV-B effect.

statistical model used for each species were treatment and enclosure nested within treatment (Table 1). Although enclosures were systematically placed, enclosure nested within treatment was treated as a random effect (Hurlbert 1984). The statistical package used for all analyses was SAS-JMP Version 3.1 for IBM (SAS Institute, Cary, N.C.)

Results

Among the seven species tested, most were insensitive to variations in UV-B (Figure 2). The biomass of the grass species *S. faberi*, *E. crusgalli* and *E. virginicus* were not significantly affected by the different levels of UV-B. The forb, *L. biennis* had a trend toward lower above-ground biomass (14%; $p = 0.0656$) under ambient UV-B. In contrast, *O. parviflora* exhibited a significant increase (10.2%; $p = 0.0009$) in total

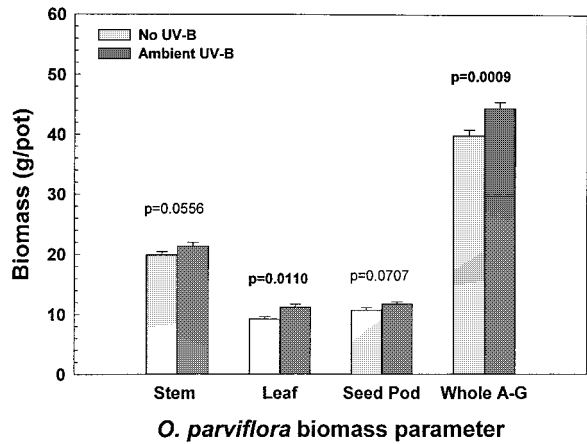


Figure 3. Above-ground biomass of *Oenothera parviflora* grown under no and ambient UV-B. Bars represent one standard error of the mean. P values in bold type indicate a significant UV-B effect.

above-ground biomass in ambient-treated plants. No significant difference was found between treatments for *V. blattaria*. The total above-ground biomass of the singular tree species studied, *Q. rubra*, was also unaffected by UV-B treatment.

Biomass partitioning between individual plant tissues was affected by UV-B only in *O. parviflora*. The most responsive component in this species was leaf biomass. For *O. parviflora*, total leaf biomass was significantly greater (18%; $p = 0.0110$) under ambient UV-B and accounted for about 44% of the difference in total above-ground biomass (Figure 3). In addition to significantly greater leaf biomass, there was also a trend towards increased stem (6.7%; $p = 0.0556$) and seed pod (9%; $p = 0.0707$) biomass. Consistent with the overall pattern of greater biomass production, *O. parviflora* also grew significantly taller (5.3%; $p = 0.0020$) under ambient levels of UV-B (Table 2). No significant difference was found in total seed pod number (Table 2). In contrast to *O. parviflora*, no significant difference was found in the above-ground biomass components of *Q. rubra* due to UV-B treatment (Table 3).

Discussion

Prior UV-B experiments suggest what characteristic biomass responses should be for plant species from various life forms. Typically, native grass species grown under variable UV-B have either higher total biomass accumulation (Musil 1995; Tosserams & Rozema 1995; Tosserams et al. 1997) or are unaf-

Table 2. Total plant height and total seed-pod number per pot for *Oenothera parviflora* under no and ambient UV-B. P values in bold type indicate a significant UV-B effect.

Parameter	No UV-B	Ambient UV-B	p-value
Total plant height (cm)	268.12	283.09	0.0020
Average per plant	89.37	94.36	
Total seed pod number	95.10	97.70	0.7433
Average per plant	31.70	32.57	

Table 3. Stem and leaf biomass per pot for *Quercus rubra* under no and ambient UV-B.

Parameter	No UV-B	Ambient UV-B	p-value
Stem biomass (g)	7.04	6.67	0.5226
Leaf biomass (g)	8.79	6.51	0.3853

ected by higher levels of UV-B (Barnes et al. 1988, 1988; Ernst et al. 1997; Musil 1995; Tosserams et al. 1996, 1997). In agreement with past research, the three grass species in our study, *S. faberi*, *E. crusgalli* and *E. virginicus*, were unaffected by the exclusion of UV-B.

Previous experiments with native forbs reveal that total biomass or the biomass of certain plant parts may be stimulated (Barnes et al. 1990; Musil & Wand 1994), decreased (Tosserams et al. 1997), or unaffected by higher levels of UV-B (Musil 1995; Tosserams et al. 1996). Consistent with the variable response reported in previous research, the forbs in this study exhibited each of the three different growth responses observed in previous experiments. A trend toward a reduction in total above-ground biomass occurred in *L. biennis* raised under the higher ambient UV-B level, *V. blattaria* was not affected by UV-B treatments, and *O. parviflora* showed a significant stimulation in growth under ambient UV-B. The magnitude of the biomass reduction (14%) for *L. biennis* in our study was less than that for forbs in a previous study (16–19%; Tosserams et al. 1997), and the magnitude of stimulation for *O. parviflora* (10%) was also less than past studies (14–36%; Barnes et al. 1990; Musil & Wand 1994; Sullivan et al. 1992). One reason for these differences may be the fact that the past studies were lampbank experiments, while our study used the exclusion method.

Though magnitudes in stimulation differ, it is intriguing that positive UV-B growth responses have been observed in *O. parviflora* in our study as well as in other plant species (Barnes et al. 1990; Musil & Wand 1994), including a species from that same genus, *Oenothera stricta* (Sullivan et al. 1992). However, the mechanisms by which any of these plants are stimulated by elevated UV-B remains unclear. One hypothesis is that stimulations of photosynthesis occur due to UV-B induced changes in leaf orientation. For instance, Tosserams et al. (1997) found that leaf orientation in plants receiving no UV-B was more vertical compared to plants receiving UV-B, and they suggested that this more planophilous orientation might allow plants to increase light interception, use available PAR to a higher degree, and thereby increase carbon fixation. A second hypothesis is that higher levels of UV-B increase biomass at the end of a growing season by improving the tolerance of some plants to water stress. For example, *Pinus* species experiencing natural water stress in the field had improved needle water relations and higher needle and total above-ground biomass at the end of the growing season when grown under elevated UV-B levels compared to water-stressed plants grown under ambient UV-B (Manetas et al. 1997; Petropoulou et al. 1995). The improved needle water relations were thought to result from stomatal effects or increases in antioxidative enzymes and suspected to contribute to the increase in biomass (Manetas et al. 1997; Petropoulou et al. 1995).

While UV-B induced reductions in water stress may explain enhanced plant growth in some studies, it is an unlikely explanation for the response of *O. parviflora* in this study because we watered the plants twice daily to the point of saturation. In contrast to the unlikely effects of UV-B on water stress in our study, morphological alterations in leaf orientation could have increased carbon fixation and growth in *O. parviflora*. However, we did not make the measurements necessary to test this idea. Since it remains unclear why the growth of some species is stimulated by higher levels of UV-B, it is apparent that future experiments should focus on these species in order to determine the physiological basis of the stimulatory response.

In our study, a more detailed examination of growth stimulation via biomass partitioning revealed that the increase in total above-ground biomass in *O. parviflora* resulted primarily from a significant increase in total leaf mass. Along with biomass alterations, *O. parviflora* also exhibited an increase in

plant height under ambient UV-B. Other native dicot species have been shown to grow taller when exposed to higher amounts of UV-B (Barnes et al. 1990), and some scientists have suggested that morphological alterations induced by higher UV-B levels, such as changes in plant height, may shift the competitive balance between species within an ecosystem (Rozema et al. 1997a,b). However, only a limited number of studies have provided direct evidence for claims that morphological alterations can modify competition (Caldwell et al. 1995; Barnes et al. 1988).

The potential importance of UV-B induced height alterations in shifting competition was demonstrated directly in studies using wild *Avena fatua* L. and *Triticum aestivum* L. under elevated UV-B (Barnes et al. 1988). In this study, elevated UV-B inhibited shoot height and leaf elongation in *A. fatua*, which allowed *T. aestivum* to overtop it, intercept more light, and achieve greater rates of canopy photosynthesis than plants growing under ambient UV-B (Barnes et al. 1988). In contrast to the differential inhibition of shoot elongation documented by Barnes et al., we found that higher levels of UV-B directly stimulated the growth of *O. parviflora* in monoculture. If *O. parviflora* responds to higher levels of UV-B in a similar manner when grown in competition, then it should gain a competitive advantage over other species whose growth is either unresponsive or inhibited.

A review of results from prior UV-B experiments on angiosperm tree species indicates that higher amounts of UV-B either lower biomass accumulation (Bogenreider & Klein 1982; Searles et al. 1995; Sullivan et al. 1994) or fail to have any effect on biomass (Bogenreider & Klein 1982; Ernst et al. 1997; Klironomos & Allen, 1995; Schumaker et al. 1997; Searles et al. 1995; Sullivan et al. 1996). In the tree species used in this experiment, *Q. rubra*, there was no alteration in total above-ground biomass with UV-B exclusion. Although our results suggest that *Q. rubra* is insensitive to UV-B, it is possible that UV-B effects in this species require more than one year to alter growth. Such cumulative effects have been observed for other long-lived tree species (Sullivan & Teramura 1992; Sullivan et al. 1994). For example, *Liquidambar styraciflua* showed no significant UV-B effects in the first year of growth, but elevated UV-B caused a reduction (19%) in leaf biomass by the second year (Sullivan & Teramura 1992). Because various *Quercus* species have ecological and economic importance in forests of the Eastern United States, it would be worthwhile to examine if cumulative UV-B

effects might also occur in *Q. rubra* or other *Quercus* species.

Overall, this investigation expands our limited knowledge of how exposure to varied levels of natural UV-B can affect the accumulation of biomass in non-agricultural plant species. Temperate-zone grass and tree species were found to be unresponsive to exclusion of UV-B. However, forbs were found to have UV-B responses that were species-specific and specific on individual plant tissues. These findings demonstrate that some forbs found in natural communities are sensitive to changes in UV-B levels and may respond to future fluctuations in the amount of this radiation, in ways that might modify population dynamics, competitive interactions, and productivity in the environments that these species inhabit.

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