

The influence of elevated ultraviolet-B radiation (UV-B) on tissue quality and decomposition of loblolly pine (*Pinus taeda* L.) needles

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Abstract

Stratospheric ozone depletion is expected to elevate the influx of ultraviolet-B radiation (UV-B) to the biosphere. Increased levels of UV-B may, in turn, alter important ecosystem processes such as decomposition. Previous studies have shown that growth under elevated UV-B can alter leaf quality in angiosperm species and thereby indirectly change subsequent rates of leaf decay. In this experiment, we determined if elevated UV-B would alter the chemical composition and decay of needle tissue from two seed sources of the gymnosperm *Pinus taeda* L. Maryland and Virginia seed sources of *P. taeda* were grown in the field for 3 years beneath lampbanks supplying either ambient, low elevated or high elevated UV-B. These levels of UV-B corresponded to 0, 16 and 25% stratospheric ozone depletion at the experimental site in Beltsville, MD (39°N). Needles were collected from six randomly chosen plants for each combination of seed source and UV-B level. The needle samples were analyzed for total C and N, UV-B absorbing compounds, and carbon fractions. Decay rates were also determined by measuring rates of CO₂ evolution from needle material decomposed under laboratory conditions. UV-B did not significantly alter the chemical composition of needles from the Virginia seed source. In contrast, needles from the Maryland seed source tended to have elevated lignin/N ratios and a lower holocellulose content when grown under the highest level of UV-B. Furthermore, while needles from the Virginia pines did not have UV-B altered decay rates, Maryland needles grown under low elevated UV-B conditions decomposed 36% more rapidly than needles from other treatments. Results from this experiment illustrate at least three characteristics about the indirect effect of UV-B on decomposition, (1) UV-B can modify decomposition of tissue from gymnosperms as well as angiosperms; (2) UV-B effects on tissue chemistry and decay may not only be species-specific but also seed-source specific; and (3) UV-B effects on decomposition may not increase with increasing UV-B dose. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Stratospheric ozone has decreased 10–11% in the northern hemisphere from 1980 to the mid-1990s and this is estimated to have increased the influx of ultraviolet-B radiation (UV-B; 280–320 nm) to the earth's surface by 10% (Herman et al., 1996; Bojkov and Fioletov, 1997; Callis et al., 1997; Kane, 1998). This elevated influx of harmful UV-B to the biosphere has the potential to alter significantly ecological processes in both agricultural and natural ecosystems (McLeod and Newsham, 1997; Rozema et al., 1997a). While numerous studies have investigated the damaging effects of UV-B in agricultural systems, fewer studies have examined UV-B effects on native plant species and related ecosystem processes (Teramura, 1990; Rozema et al., 1997a). One important ecosystem process, which may be altered by an increased UV-B flux, is the decomposition of plant litter (Caldwell, 1989; Caldwell et al., 1995).

Litter decomposition may be affected directly or indirectly by elevated UV-B. Direct effects of UV-B on litter decay are probably more important in high-irradiance habitats, such as deserts, where UV-B can photochemically degrade plant compounds or hinder microbial growth (Moorehead and Reynolds, 1989; Moorehead and Callaghan, 1994; McKay et al., 1994). However, in many ecosystems shading or burial of litter in the soil may minimize the direct effects of UV-B. For example, Brown et al. (1994) used a Robertson–Berger-type meter to measure UV-B (weighted using the action spectrum for human sunburn) and found that UV-B transmittance near the floor of an eastern deciduous forest was about 30% of incident radiation during the leafless season and only 1–2% of incident radiation under a closed canopy. As a result, we expect that the indirect effects of UV-B should have a more important role than direct effects in modifying rates of decay in temperate forest and old-field ecosystems.

UV-B can indirectly affect decomposition by altering the production of chemical compounds in the tissues of growing plants. Of significance to litter decay are modifications in tissue chemistry

that result from changes in overall carbon allocation or from changes in general phenylpropanoid metabolism and the pathways branching from it which produces specific secondary carbon compounds (Wellman et al., 1976; Hahlbrock and Grisebach, 1979; Chappell and Hahlbrock, 1984; Caldwell, 1989). These secondary compounds include flavonoids, lignin, and other phenolics (Ebel and Hahlbrock, 1982). Of these secondary compounds, the concentration of flavonoids frequently increases in plants subject to elevated UV-B since flavonoid synthetic enzymes are specifically induced by this type of radiation (Hahlbrock and Grisebach, 1979; Teramura, 1983; Wellman, 1983). In contrast, it is relatively unknown how UV-B affects the production and concentration of other phenolic compounds in plant tissues. It has been speculated that many chemicals important to decomposition may be altered by UV-B induced changes in the general phenylpropanoid pathway (Paul et al., 1997; Rozema et al., 1997a,b), and recent studies have confirmed that such changes can occur. However, the specific compounds altered by UV-B and the direction of the change in composition are not consistent among existing studies. For example, after growing plants under levels of UV-B that simulated a 15% reduction in stratospheric ozone, Gehrke et al. (1995) observed significant decreases in the α -cellulose (18.8%) and no change in the lignin content of *Vaccinium uliginosum* L. leaf litter. However, Rozema et al. (1997c) found a significant increase in α -cellulose (11.1%) and lignin (35.9%) content in *Calamagrostis epigeios* L. Roth under levels of UV-B simulating a 15% reduction in stratospheric ozone. Furthermore, Newsham et al. (1999) found no change in either holocellulose or lignin content and only a trend towards lower lignin/N ratios in leaves from *Quercus robur* L. after growth under levels of UV-B that simulated an 18% depletion in stratospheric ozone. Finally, Yue et al. (1998) observed that supplemental UV-B simulating 12, 20, or 25% ozone depletion increased the nitrogen content of above-ground biomass and the holocellulose content in leaves of *Triticum aestivum* L.

With only this limited number of experimental results, it is uncertain how UV-B may alter the

overall content of carbon, nutrients, and important secondary compounds in plant tissue. However, any change in the concentration of chemical components in plants may strongly affect rates of litter decay because the chemical composition of litter tissue determines its quality as an energy resource for decomposer organisms and can thereby influence its rate of mass loss and nutrient release (Swift et al., 1979; Aber and Melillo, 1991; Coûteaux et al., 1995). In particular, the lignin content, the lignin/N ratio and the C/N ratio of litter are often useful predictors of litter decay rates over time (Meentemeyer, 1978; Melillo et al., 1982, 1989; McClaugherty and Berg, 1987; Taylor et al., 1989). Additional modifiers of litter decay include other secondary compounds such as phenolic acids and tannins (Horner et al., 1988). These polyphenolic compounds affect the palatability of litter or inhibit microbial growth and colonization in ways that reduce rates of decay (Harrison, 1971; Swift et al., 1979).

Four published studies have examined if UV-B indirectly modifies decompositional processes in terrestrial plants. Gehrke et al. (1995) observed that alterations in the biochemical composition of shrub litter caused by elevated UV-B treatment were associated with a significant decrease (5.6%) in the relative mass loss over 62 days and a depression (35%) in the release of microbial CO₂ during the initial stages of decay. Rozema et al. (1997c) also found that UV-B altered the chemical composition of grass tissue in ways that appeared to reduce significantly (3.0%) mass loss after 60 days of decay. In contrast to previous studies, Newsham et al. (1999) found that elevated UV-B increased (3.8%) mass loss of *Q. robur* leaves after 6 and 16 months of decomposition, although only a marginally significant change in litter composition was apparent. In addition, Yue et al. (1998) observed that leaf and stem material of *T. aestivum* grown under elevated UV-B stimulated the loss of organic carbon during 60 and 100 days of decay. Thus, these results support the hypothesis that UV-B alterations in leaf tissue occur in a manner that can either reduce or stimulate subsequent rates of decomposition (Caldwell, 1989; Caldwell and Flint, 1994; Teramura, 1990).

Since all previous investigations of the indirect effects of UV-B on plant decomposition have been limited to angiosperms, we wanted to broaden our understanding of this topic by examining whether exposure to elevated UV-B during growth would also affect the chemical composition and subsequent decay of tissue from a gymnosperm species. We chose *Pinus taeda* L. (loblolly pine) because this species is physiologically responsive to elevated levels of UV-B (Sullivan and Teramura, 1988, 1989, 1992, 1994; Sullivan et al., 1996). In earlier experiments, elevated UV-B has been shown to reduce total biomass, height, and net photosynthesis in the greenhouse and also reduce total biomass and needle length in the field with effects appearing to accumulate as plants aged. Therefore, due to the apparent sensitivity of *P. taeda* to UV-B enhancement, we hypothesized that elevated levels of UV-B would alter *P. taeda* needle chemistry through physiological effects in ways that would indirectly modify their decomposition.

2. Materials and methods

2.1. Plant growth

As part of a large UV-B growth study (Sullivan and Teramura, 1992), *P. taeda* L. from two open-pollinated seed sources, Virginia and Maryland, were grown in the field under supplemental UV-B radiation for three consecutive growing seasons from 1987–1989. Trees were grown at a field site located 5 km north of College Park, MD on a farm owned and operated by the US Department of Agriculture. Seeds were provided by the Maryland State Nursery and the United States Forest Service Tree Seed Laboratory (Macon, GA, USA). Before planting, seeds were stratified for 30 days at 3°C. Seeds were then germinated in the greenhouse in ‘Cone-tainers’ (Conetainer Nursery, Wilsonville, OR, USA) in an acid peat mixture mulched with pine straw.

Seedlings were transplanted 6 weeks after germination, and the plants were grown in pots containing a mixture of milled pine bark, peat and sand (3:1:1 by volume). Pots were 8-l in size for

the first growing season and 20-l for the following two seasons. Transplanting to larger pots was done during the winter before the spring flush of the second growing season. The pots were buried at ground level and mulched with straw to minimize soil temperature variation. The experiment was structured as a complete randomized block design with three UV-B treatments (two supplemental treatments and one ambient treatment) and four replicates of each treatment. Beneath each lamp frame, a total of 20 plants from each seed source were placed at 20-cm intervals along rows spaced 25-cm apart during the first growing season. During the second and third growing season, the rows of seedlings were spaced 40 and 80-cm apart. These planting densities were chosen to reduce shading by neighboring plants throughout the 3-year study.

Artificial UV-B radiation was supplied by filtered Q-Panel UV-B-313 sunlamps that were suspended above the plants and oriented perpendicular to the planting rows (Teramura et al., 1990). Lamps were fitted with 50-mm-wide mini reflectors with lamp ballasts and timers remotely fixed to minimize shading. Total daily photosynthetic photon flux density (400–700 nm) under the lamps was approximately 90% of that above the lamps. The entire lamp support system was suspended from wires stretched between 3-m-tall poles located at the end of the planted rows. Plants were irradiated daily using a 'square-wave' treatment (McLeod, 1997) for 6 h centered around solar noon.

To achieve the desired levels of UV-B, lamps were filtered with either 0.13-mm polyester film (transmission down to 320 nm) for the ambient 'control' condition or 0.13-mm-thick cellulose diacetate (transmission down to 290 nm) for supplemental UV-B radiation treatments. There was no supplemental irradiance under lamps filtered with polyester, so plants beneath these lamps received only ambient levels of UV-B ($8.4 \text{ kJ m}^{-2} \text{ UV-B}_{\text{BE}}$ on the summer solstice, June 22). The radiation from lamps that was filtered through cellulose diacetate supplied a weighted daily supplemental irradiance of either 3.1 or $5.0 \text{ kJ m}^{-2} \text{ UV-B}_{\text{BE}}$ on the summer solstice using the generalized plant action spectrum (Caldwell, 1971) normalized to

300 nm. Thus, plants beneath these lamps received supplemental doses plus ambient levels of UV-B. The increased UV-B levels achieved were similar to those that would be anticipated at Beltsville, MD, USA (39°N) with a 16 or 25% stratospheric ozone depletion during a cloudless day on the summer solstice (Green et al., 1980). Different UV-B treatments were obtained by varying the distance between the lamps and the tops of the plants (a distance of 0.75 and 1.0 m was used for 5.0 and $3.1 \text{ kJ m}^{-2} \text{ UV-B}_{\text{BE}}$, respectively). Lamp positions were adjusted weekly as plants grew and the UV-B irradiance was adjusted monthly to correct for seasonal changes in ambient UV-B as calculated by Green et al. (1980). Cellulose diacetate filters were pre-solarized for 8 h and changed weekly to assure uniformity of UV-B transmission. Prior to the initiation of the experiment each year, sunlamps were pre-burnt and matched for the desired spectral irradiance as described by Teramura (1981). Spectral irradiance beneath the lamps was measured with an Optronics Model 742 spectroradiometer equipped with a double monochromator with dual holographic grating and interfaced with a Hewlett–Packard 85 printing calculator. Calibration of the spectroradiometer was performed using a National Institute of Standards and Technology traceable 1000-W tungsten halogen lamp, and wavelength alignment was checked with mercury emission lines using a mercury lamp.

In this UV-B decomposition experiment, we used needle material collected from individual plants after the third growing season. Previous analyses for other purposes consumed most of the plant tissue produced in the third year (Sullivan and Teramura, 1992). However, from plant material harvested after the third season (six plants of each seed source per lampbank), needle samples remained from three randomly chosen plants of each seed source under two replicate lampbanks per UV-B level. This gave us a total of six needle samples for each of the three UV-B treatment levels that we could analyze for each seed source in this UV-B decay study (three random plants per lampbank \times two lampbanks UV-B level = six needle samples per UV-B level). The needles from the third year used in our experiment contained

mixtures of needles of various ages and flushes. Primary needles were gone by the time plants were harvested (October/November). Therefore, all collected needles were fascicle and not primary needles. In addition, needle samples collected across UV-B treatments contained similar amounts of needles from each age class, since there were no obvious effects on phenology between treatments. As a result, UV-B effects on chemistry and decay should not have been confounded due to differential representation of needle age classes across treatments. Once needles were collected, subsamples were dried (70°C for 2 weeks), analyzed chemically, and decomposed under controlled laboratory conditions to determine whether there were UV-B effects on tissue chemistry and decay rates.

2.2. Chemical analysis of needles

Needles were ground to pass through 20 mesh screen in a Wiley mill, and subsamples of the ground tissue were analyzed for total N and C, proximate carbon fractions (non-polar and polar extractable carbon compounds, holocellulose, and lignin), and UV-B absorbing compounds. Total N and C were determined by Dumas combustion using a Carlo Erba 1500 N, C, S elemental analyzer. Proximate carbon fractions were determined using the procedure of Melillo et al. (1989). The content of UV-B absorbing compounds (flavonoids and related compounds) was analyzed in acidified methanol extracts according to Day (1993), with the exception that the absorbance values were measured on a per gram basis.

2.3. Laboratory decomposition assay

A 1 g subsample of the ground needles was placed into separate 160-ml serum bottles. The material was moistened with 2 ml of general microbial inoculum (Gehrke et al., 1995) prepared from forest soil collected at the Core Arboretum in Morgantown, WV. After treatment, all bottles were sealed with rubber stoppers, which were pierced with a syringe needle fitted with a gas-tight one-way valve. These valves were left open between measurements to allow gas exchange.

Initial weights of the bottles were recorded and used to correct for moisture loss. Moisture levels were maintained by periodically adding distilled water to compensate for any reduction in mass.

All serum bottles were placed in a bench-top, constant temperature (30°C) water bath and decomposed for 3 months in the lab under ambient lighting conditions. Rates of CO₂ evolution were measured weekly beginning 1 week after the initial placement of litter. Prior to each measurement, the serum bottles were flushed with air, and the valves were sealed. An initial measurement of the amount of CO₂ in each bottle was taken by extracting a 1 ml gas sample and injecting it into a Li-Cor infrared gas analyzer (LI-6200 and LI-6250; LiCor Inc., Lincoln, NE, USA) adapted for single injection use with a piece of vacuum tubing acting as a sample injection port. The sealed serum bottles were incubated for 2 h at 30°C, after which a final 1 ml gas sample was taken and analyzed in a similar manner. After each final measure, the valves were re-opened, and the serum bottles were placed back into the incubator.

The total amount of CO₂ evolved in each serum bottle was calculated by multiplying the change in CO₂ concentrations by the total air volume of the bottle. The total air volume of a bottle was determined by injecting a known amount of air into each and measuring the pressure change using a pressure transducer (Parkin et al., 1984). Atmospheric pressure and temperature were recorded during each measuring period to calculate the respiration rate and express it as CO₂ released per hour per gram of original dry weight.

2.4. Statistical analysis

To determine if UV-B affected needle chemistry and indirectly affected the rate of needle decomposition, separate nested one-way analysis of variance (ANOVA) tests were performed on chemical measurements for each seed source (Table 1A), and separate nested analysis of variance with repeated measures (ANOVAR) tests were performed on laboratory decomposition data (Table 1B) for each seed source. For all statistical tests, effects with a value of $P \leq 0.05$ were considered

statistically significant, while effects with a value of $P > 0.05$ but ≤ 0.10 were described as trends.

3. Results

Among the two types of loblolly pine that were tested, elevated UV-B did not significantly alter the chemical composition or decay rate of needle material from the Virginia seed source (Tables 2 and 4). In contrast, the Maryland seed source showed subtle changes in tissue chemistry and a significant modification in the rate of decomposi-

tion due to elevated levels of UV-B (Tables 3 and 4). While most chemical parameters were unaffected, there were trends towards a higher lignin/N ratio (11% greater) and a lower holocellulose content (7%) in tissue grown under the high elevated UV-B treatment (Table 3). However, the shift towards higher lignin/N ratios and reduced holocellulose in needle tissue did not correspond to modified decomposition rates in the high elevated material. Instead, we found that the decomposition of needles grown under the low elevated UV-B levels released CO_2 at higher rates ($\approx 36\%$) than decomposing needle material from either of

Table 1
Statistical models for data analysis

Effect	Df	<i>E</i> (MS)	Den (MS)	Effect
<i>(A) One way nested ANOVA used for the chemical measurements made on each seed source</i>				
Treatment	2	$\sigma^2 + \sigma_{B[T]}^2 + K_T^2$	Bank (treatment)	Fixed
Bank (treatment)	3	$\sigma^2 + \sigma_{B[T]}^2$	Error	Random
Error	12	σ^2		
C total	17			
<i>(B) Nested ANOVA used for the laboratory decomposition data of each seed source</i>				
Treatment	2	$\sigma^2 + \sigma_{B[T]}^2 + K^2$	Bank (treatment)	Fixed
Bank (treatment)	3	$\sigma^2 + \sigma_{P[B,T]}^2 + \sigma_{B[T]}^2$	Plant (bank, treatment)	Random
Plant (bank, treatment)	12	$\sigma^2 + \sigma_{P[B,T]}^2$	Error	Random
Day	10	$\sigma^2 + \sigma_{D*B[T]}^2 + K_D^2$	Day*bank (treatment)	Fixed
Day*treatment	20	$\sigma^2 + \sigma_{D*B[T]}^2 + K_{DT}^2$	Day*bank (treatment)	Fixed
Day*bank (treatment)	30	$\sigma^2 + \sigma_{D*B[T]}^2$	Error	Random
Error	120	σ^2		
C total	197			

Table 2
Mean values for chemical parameters of the Virginia seed source of loblolly pine (*P. taeda* L.) grown under varied levels of UV-B^a

Parameter	Ambient UV-B	Low elevated UV-B	High elevated UV-B	Treatment <i>P</i> -value
Total C (%)	47.72	49.91	48.95	0.6030
Total N (%)	2.42	2.46	2.57	0.7710
C:N	19.78	20.56	19.19	0.6914
Non-polar (%)	4.76	5.38	5.94	0.1117
Polar (%)	33.37	33.51	34.17	0.3338
Lignin (%)	28.73	27.93	27.47	0.2112
Holocellulose (%)	33.42	33.18	32.42	0.5115
Lignin:N	11.93	11.52	10.79	0.4514
UV-B absorbing compounds (<i>A</i> per g, 300 nm)	117.44	108.50	110.66	0.7875

^a Means are based upon six samples per UV-B treatment level.

Table 3

Mean values for chemical parameters of the Maryland seed source of loblolly pine (*P. taeda* L.) grown under varied levels of UV-B^a

Parameter	Ambient UV-B	Low elevated UV-B	High elevated UV-B	Treatment <i>P</i> -value
Total C (%)	50.06	50.23	50.42	0.8443
Total N (%)	2.49	2.45	2.33	0.5548
C:N	20.09	20.84	21.85	0.4519
Non-polar (%)	4.80	4.42	5.08	0.7665
Polar (%)	31.92	33.55	33.66	0.2906
Lignin (%)	28.44	28.62	29.40	0.4626
Holocellulose (%)	34.84	33.41	31.86	<i>0.0770</i>
Lignin:N	11.37	11.84	13.08	<i>0.0633</i>
UV-B absorbing compounds (<i>A</i> per g, 300 nm)	104.72	119.03	102.93	0.4052

^a Means are based upon six samples per UV-B treatment level. *P* values in italics indicate a trend.

the other two UV-B treatments, despite the absence of any treatment effects on tissue chemistry (Table 4; Fig. 2). Finally, in both seed sources we observed a similar temporal pattern of decay: an initial period of increasing decay rates (days 11–39) followed by a sharp decrease in decomposition on day 55 and then a second period of increasing decay rates followed by a subsequent decline from days 60 through 90 (Figs. 1 and 2).

4. Discussion

The results from this study illustrate at least three features about the indirect effect of UV-B on decomposition. First, UV-B can alter the decay of tissue from gymnosperm as well as angiosperm species. All previous studies of this type have used tissue from angiosperms, so our observations represent the first data available for gymnosperms. In comparison with results of prior UV-B decomposition experiments, the significant increase we measured in the decay of some loblolly needles (the Maryland seed source grown under low elevated UV-B) is qualitatively consistent with the increased decay rates observed by both Newsham et al. (1999) for *Q. robur* leaves and Yue et al. (1998) for *T. aestivum* litter. However, our results contrast sharply with those of Gehrke et al. (1995), Rozema et al. (1997c) who found that growth under elevated UV-B slowed subsequent decay. Thus, from the varied results of

these existing studies, no general conclusions can be drawn about either the direction or magnitude of the indirect effects of UV-B on litter decomposition. Furthermore, comparisons between existing studies are complicated by differences in the actual dose of UV-B received by the plants, differences in growing conditions, and differences in the methodology used to measure decay rates (e.g. lab vs. field assays).

The second feature we observed about the indirect effects of UV-B on tissue chemical composition and decay was that these effects could be seed source specific. In this study, the decay of tissue from the Virginia seed source was unre-

Table 4

Statistical results of nested ANOVAR for Virginia and Maryland seed source laboratory decomposition data^a

Seed source	Effect	<i>P</i> value
Virginia	Treatment	0.6249
	Bank (treatment)	0.4002
	Plant (bank, treatment)	< 0.0001
	Day	< 0.0001
	Day*treatment	0.3890
	Day*bank (treatment)	0.8957
Maryland	Treatment	0.0016
	Bank (treatment)	0.9945
	Plant (bank, treatment)	< 0.0001
	Day	< 0.0001
	Day*treatment	0.7256
	Day*bank (treatment)	0.9155

^a *P* values in bold type indicate a significant UV-B effect.

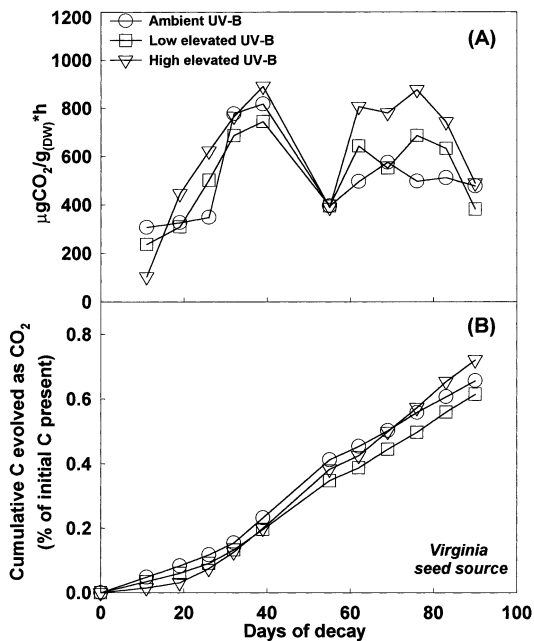


Fig. 1. Temporal patterns of elevated UV-B effects on CO₂ evolution over a 90-day decay period for the Virginia seed source of *P. taeda*. (A) Individual mean measures of CO₂ evolution (µg CO₂ per g_{DW} per h) at each time of measurement. (B) The cumulative percent of the initial amount of C present that was evolved as CO₂ during the incubation. Rates measured at the beginning of each time interval were used to estimate CO₂ evolution during the entire interval, except for days 0–11 when day 11 rates were used.

sponsive to the level of UV-B under which the plants were grown. In contrast, tissue from the Maryland source decayed 36% more rapidly when grown under the intermediate (low elevated) level of UV-B. Previous studies indicate that interspecific differences appear to be common for the indirect effects of UV-B on litter chemical composition and decay (Gehrke et al., 1995; Rozema et al., 1997c; Yue et al., 1998; Newsham et al., 1999). This study, however, reveals that these parameters also exhibit intraspecific variation in response to UV-B when varied seed sources of the same species are grown under the same experimental conditions. This additional aspect of intraspecific variation further complicates attempts to make general conclusions about UV-B effects on plant decay.

The third feature we observed from this study was that the indirect effect of UV-B on tissue decay did not increase monotonically with increasing UV-B levels — a further complication when comparing studies where the actual doses of UV-B were not reported. While the majority of previous studies have examined the effect of UV-B on decay by using a single level of elevated UV-B (Gehrke et al., 1995; Rozema et al., 1997c; Newsham et al., 1999), one recent study by Yue et al. (1998) used four levels of UV-B and found that decay rates of plant tissue consistently increased in plants that were grown under sequentially higher levels of supplemental UV-B. Therefore, we expected that the UV-B effect in *P. taeda* would be heightened as the UV-B dose increased. However, in contrast to our expectations, we

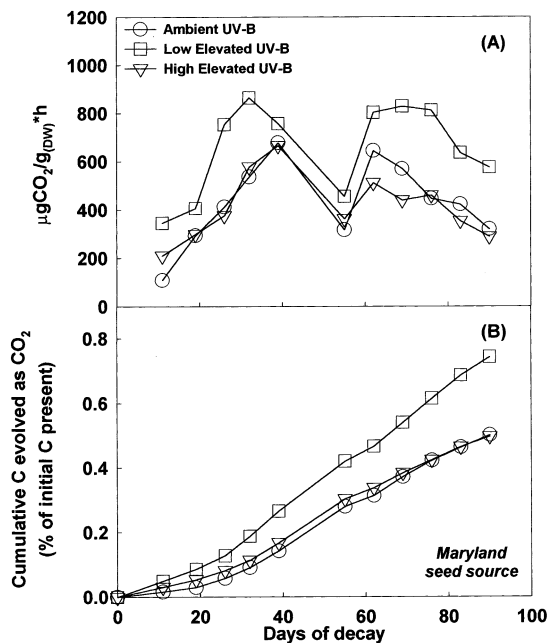


Fig. 2. Temporal patterns of elevated UV-B effects on CO₂ evolution over a 90-day decay period for the Maryland seed source of *P. taeda*. (A) Individual mean measures of CO₂ evolution (µg CO₂ per g_{DW} per h) at each time of measurement. (B) The cumulative percentage of the initial amount of C present that was evolved as CO₂ during the incubation. Rates measured at the beginning of each time interval were used to estimate CO₂ evolution during the entire interval, except for days 0–11 when day 11 rates were used.

found that the effects of UV-B on plant decomposition did not increase in this manner in *P. taeda*. Thus, for decay in this, and perhaps other species, UV-B effects may be apparent at lower elevated doses but not higher ones. While such a phenomena has been noted for at least a few other plant parameters, such as seed abortions and seed mass in *Brassica rapa* L. (Aaa RCB seeds; Demchik and Day, 1996) and seed yield and seed mass in *Glycine max* L. Merr. (Teramura et al., 1990), we find this occurrence novel since such a pattern is both new with respect to the indirect effects of UV-B on plant tissue decay and decidedly different than the pattern observed in the only other UV-B decomposition study which tested multiple levels of enhanced UV-B. Given the results of our study, it is unclear why tissue from the Maryland seed source decomposed more quickly only when it was grown under an intermediate level of elevated UV-B exposure. However, our data did not support the hypothesis that it was a direct result of measurable changes in tissue chemistry. If changes in tissue chemistry were important, then needles from the Maryland seed source that tended to have a higher lignin/N ratio should have decomposed more slowly (Melillo et al., 1982; Taylor et al., 1989), but they did not. Furthermore, we observed a significant change in decomposition in the absence of any detectable difference in tissue chemistry. Due to the limited nature of this study, we can only offer three hypotheses that may account for why this occurred, (1) changes in chemistry, too subtle to be detected by the methods we employed, acted collectively to alter the rate of decay; (2) an important modification of tissue chemistry occurred in parameter we did not measure; (3) alterations of needle cellular morphology (e.g. cell thickness or toughness) may have occurred which led to altered rates of decomposition.

One additional feature observed in this study was that the decay of tissue from both seed sources appeared to follow similar temporal patterns. Decomposition of both seed sources was characterized by an initial period of increasing decay rates (days 11–39). This period was then followed by a sharp decrease in decomposition (day 55) and then a second period of increasing

and then decreasing decay rates (days 60–90; Figs. 1 and 2). Based on other studies which found similar patterns of microbial respiration (Taylor et al., 1989), a likely explanation for the temporal pattern we observed was that the microbial population initially grew rapidly while they decomposed fresh litter material. The rates of decomposition then declined as the composition of the microbial community shifted (ca. day 55) in response to a reduction in the supply of labile organic matter. Finally, decay rates exhibited a short-lived increase from the utilization of dead microbial biomass by the new microbial community followed by a substantial drop in respiration due to an increasing reliance on more recalcitrant sources of carbon. If our explanations for the observed temporal pattern are correct, then the type of carbon compounds affected by elevated levels of UV-B (whether labile or recalcitrant) may determine when the indirect effects of UV-B will appear and whether they may be ecologically significant at the ecosystem level.

5. Conclusions

The results of this study, in addition to those from previous studies, provide some support for the hypothesis that exposure to elevated levels of UV-B can alter the chemical composition and decay rate of plant material. However, we believe that the variable and often conflicting nature of the existing data, both in terms of the direction and magnitude of the observed effects, strongly indicates that more research is required before any general pattern emerges and before we can properly assess the ramifications of these indirect UV-B effects, if any, at the ecosystem level.

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