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A meta-analysis of the responses of woody and herbaceous plants to elevated ultraviolet-B radiation

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ABSTRACT

Numerous studies have examined plant responses to elevated ultraviolet-B radiation at the species level. More than 140 studies conducted within the past three decades were collected for meta-analysis to generalize and examine overall responses of two main life-forms, woody plants and herbaceous plants under two supplemental UV-B levels. The analysis suggested that both life-forms would suffer an overall negative effect in total biomass under the two UV-B levels, and the reduction was 7.0–14.6% of the value at ambient UV-B radiation. Comparing the overall responses under the high supplemental UV-B level with those under the low supplemental UV-B level, woody plants showed no significant changes in any variables. As opposed to this, decreases in herbaceous plant height and specific leaf area as well as increase in herbaceous UV-B-absorbing compounds under the higher UV-B level were significantly greater than those under the lower UV-B level. With continued increases in UV-B levels, the two life-forms would show different response strategies for their different intrinsic capabilities to resist UV-B damage. Woody plants would not invest in large additional amounts of UV-B-absorbing compounds, while herbaceous plants would need to induce stronger defense mechanisms to protect themselves from the associated detrimental effects of UV-B radiation. A higher number of response variables were significantly affected by UV-B radiation for herbaceous plants than for woody plants. Most of the studied variables were not affected significantly under elevated UV-B for woody plants and exhibited very large confidence intervals. Further studies should investigate if the response to elevated UV-B radiation varies between different functional groups of woody species. To sum up, we suggest that as UV-B radiation continues to increase, grassland ecosystems should receive more attention for future vegetation management.

1. Introduction

Ozone depletion and the resultant elevated levels of solar ultraviolet radiation (hereafter "UV") are important factors that underlie global changes and have spurred a significant amount of research (Bowman, 1988; Caldwell et al., 2003; EEAP, 2008). Relative to conditions from 1979 to 1992, the Goddard Institute for Space Studies (GISS) estimated that the maximum increase in the annual Northern Hemispheric UV dose will be 14% in 2010–2020, whereas a 40% enhancement is expected between 2010 and 2020 in the Southern Hemisphere (Taalas et al., 2000, 2002; Haapala et al., 2009). With respect to the conservation of biodiversity, these estimates provoked the urgent need for research that evaluates the effects of UV-B on plant processes (Day, 2001). Numerous independent species level studies have assessed the effects of UV-B radiation and several comprehensive reviews have concluded that the commonly observed effects of UV-B on plants include changes in growth, development and morphology, alterations in transpiration and photosynthesis, and damage to DNA, proteins and membranes (Björn et al., 1999; Rozema et al., 2002; Björn, 2007; Caldwell et al., 2007).

Previous traditional reviews on the effects of UV-B were mostly qualitative and had poor statistical power, generally presenting lists of effects and using the reported statistical significance of each study to assess the effect strength of UV-B radiation (Rosenberg et al., 2000; Bancroft et al., 2007). Meta-analysis techniques could avoid the subjectivity of traditional reviews and provide a quantitative statistical means of integrating independent results from a number of publications (Gurevitch and Hedges, 2001; Ainsworth et al., 2007; Lei et al., 2007). In recent years, meta-analysis has been increasingly applied to identify broad trends or summarize different plant responses in several aspects of large-scale ecology and global change (Körner et al., 1997; Curtis and Wang, 1998; Kerstiens, 2001; Zheng and Peng, 2001; Root et al., 2003; Zvereva and Kozlov, 2006).

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Searles et al. (2001) provided the first quantitative estimates using meta-analysis of UV-B effects in field-based studies on vascular plants. Dormann and Woodin (2002) demonstrated the effects of increasing UV-B on Arctic plants by performing a meta-analysis of field experiments in which plants were divided into different functional types.

Scientists have demonstrated significant inter- and intra-specific variation in plant responses to enhanced UV-B radiation (Tosserams et al., 1997; Smith et al., 2000; Heisler et al., 2003; Yao et al., 2008). To generalize and incorporate overall plant responses to elevated UV-B and forecast large-scale vegetation processes, the responses of plant species should be grouped by functional types rather than studied at the species level only (Gitay and Noble, 1997; Dormann and Woodin, 2002). For example, vascular higher plants were split into two main life-forms, woody and herbaceous plants, to predict plant effects on ecosystems in some studies (Day et al., 1992; Chapin et al., 1996; Weng and Zhou, 2005). Their different responses to elevated UV-B levels may have far-reaching consequences for vegetation patterns and ecosystem composition and function (Caldwell et al., 1998).

A comparison of diverse plant groups in the Rocky Mountains found that herbaceous dicotyledonous species were the least effective at attenuating UV-B, followed in order of increasing efficacy by woody dicots, grasses, and conifers (Day et al., 1992). Some studies showed that woody plants were susceptible to UV-B irradiation (Sullivan and Teramura, 1992) and such effects may be cumulative (Naidu et al., 1993), though others found even extremely large increases in UV-B radiation were unlikely to have negative effects on growth and photosynthesis in some woody plants (Bassman et al., 2002; Trošt-Sedej and Gaberščik, 2008). Few direct and systematic studies of woody and herbaceous responses to elevated UV-B have been conducted to date. Therefore, it was still necessary to integrate existing independent studies to test if plant life-forms respond in different ways to elevated UV-B radiation.

In this study, we applied a meta-analytic approach to investigate the different responses of two main life-forms, woody plants and herbaceous plants, to two elevated UV-B levels with respect to biomass accumulation, morphology and physiology. We addressed the following questions: (1) What were the overall responses of the two plant life-forms to the two elevated UV-B levels; (2) Was there any difference in the overall responses to the same elevated UV-B level between the two plant life-forms; (3) Was there any change in the overall responses for the same life form as UV-B radiation was elevated from the low supplemental level to the high supplemental level; and (4) What changes would their different responses to elevated UV-B radiation indicate for vegetation patterns under elevated future UV-B levels?

2. Materials and methods

2.1. Database and suitability criteria

We searched publications listed in the Life Science Collection during the past three decades using “ultraviolet-B” or “UV-B” as keywords and collected all articles that reported vascular higher plant responses to elevated UV-B exposure. In total, more than 800 publications were screened, 142 of which were finally accepted for the analysis. We selected articles according to the following criteria: (1) the data must have been obtained from manipulated experiments with appropriate control treatments under ambient UV-B radiation and experimental treatments under supplemental UV-B radiation; (2) the response variables recorded must have been at least one of the 15 variables listed in Table 1, which were classified into two general categories (biomass/morphological and physiological, Table 1), and had to be measured and expressed within the study. It should be especially noted that effect sizes of biomass variables were expressed on a biomass basis but not on a delta biomass basis; (3) the means, some measures of variance (SD, SE or confidence intervals) and the sample sizes of every variable in control and experimental groups must have been reported in numerical or graphical terms, or be available from the authors (Koricheva et al., 1998); (4) only one measurement per treatment of a given species in each study could be used because every point used in meta-analysis must be independent (Curtis and Wang, 1998). For instance, when particular response variables of a plant species were measured several times within a paper, the last sampling date was chosen since global change is often long-term (Treseder, 2004). In addition, for the studies that employed seedlings of different ages, the results from the oldest were selected. If the responses to multiple environmental factors such as drought and CO_2 were assessed along with UV-B effects, only data from the baseline control conditions for elevated UV-B were used (Searles et al., 2001).

Table 1
List of general categories of plant response variables reported on in the meta-analysis.

Category	Abbreviation	Parameter name
Biomass and morphological variables	Bl	Leaf biomass
	Br	Below-ground biomass
	Bs	Above-ground biomass
	Bt	Total biomass
	R/S	Root:shoot ratio
	LA	Leaf area
	H	Plant height
	SLA	Specific leaf area
Physiological variables	Abs	UV-B-absorbing compound
	a/b	Chlorophyll a/b
	Chl	Total chlorophyll content on a mass basis
	Chla	Chlorophyll a content on a mass basis
	Chlb	Chlorophyll b content on a mass basis
	Cm	Carotenoid contents on a mass basis
	Ph	Photosynthesis rate on an area basis

Our final database consisted of results from 142 studies that were consistent with our selection criteria, reported in more than 50 different journals, of which 21 studies had already been included in the review of Searles et al. (2001) while 121 studies were new. The studies covered a wide range of species, among which 38 were woody plants and 96 were herbaceous plants. The dwarf shrubs, although belonging to woody plants, were included in the herbaceous plant group in our study given their life-history traits (Zvereva et al., 2008). The selected studies were conducted across a wide range of latitudes. Specifically, 51 were performed between 0 and 35° latitude (including 35°), 48 between 35 and 45° latitude (including 45°), and 43 at latitudes higher than 45°. Among the collected studies, approximately 55% were conducted under field conditions while the rest were performed in growth chambers or greenhouses.

2.2. Meta-analysis steps and partition groups

At present, UV-B trends can be established only indirectly from calculations based on ozone trend data. In other words, every 1% decrease in the ozone layer is estimated to correspond to an increase of about 2% of UV-B radiation that reaches the surface of the planet (Scotto et al., 1988; Herman et al., 1996; Goettsch et al., 1998). To identify general plant responses to different elevated UV-B levels, the supplemental UV-B treatments were divided into two categories: relatively low (18–40% of ambient UV-B radiation or 9–20% O_3 depletion) and high (>40% of ambient UV-B radiation, or >20% O_3 depletion). The upper limit of the high intensity treatment was set to be twice the ambient UV-B level. Plants were then partitioned into two life-form groups (woody and herbaceous) in order to analyze their different responses to elevated UV-B. We also tested for effects of several further categorical variables such as latitude of study sites, the duration of the UV-B treatment and type of exposure facility (growth chamber, greenhouse or field condition); however, these additional variables were not discussed here as they showed little or no between-group heterogeneity and several plant response variables (especially for woody plants) did not have large enough sample sizes for statistical analysis.

Meta-analysis was carried out using the statistical software Meta Win 2.0 (Rosenberg et al., 2000). To estimate treatment effects, the natural log of the response ratio was calculated for each study as $\ln R = \ln (X_e/X_c)$, where X_e and X_c were the mean response values for supplemental UV-B radiation and ambient UV-B radiation, respectively (Rosenberg et al., 2000). This value was reported as the mean percentage change ($D\ (\%) = (e^{\ln R} - 1) \times 100\%$) from ambient control. Positive percentage change indicated an increased response to elevated UV-B exposure, while negative value indicated a decreased response (Ainsworth et al., 2002). A random effects model was used based on the assumption that differences among studies within a class were due to both sampling error and random variation (Valkama et al., 2006). In this model, it was assumed that studies differed by both sampling error and by a random component in effect sizes between studies, called "pooled study variance" (Rosenberg et al., 2000; Morales and Traveset, 2009). Additionally, normal quantile plots with confidence intervals (CIs) were explored to test the assumption of normality, which was the basis of the meta-analytic procedure; deviations from linearity indicate deviations from normality (Rosenberg et al., 2000; Morales and Traveset, 2009). Elevated UV-B radiation was considered to have a statistically significant effect on a given variable if the 95% confidence interval of the mean effect size did not overlap with zero (Gurevitch and Hedges, 1993, 2001; Kulmatiski et al., 2008; Valkama et al., 2009). Differences in the percentage changes of the response variables between the two plant life-forms were tested by calculating between-group heterogeneity (Q_b) (Valkama et al., 2008; Zvereva et al., 2008), and the significance of the Q_b test was evaluated using a standard chi-square table (Kulmatiski et al., 2008). The variation in effect sizes between woody and herbaceous variables was considered to significantly differ if their 95% CIs did not overlap and the significance was established at the $P < 0.05$ level (Gurevitch and Hedges, 1993; Wang, 2007).

3. Results

3.1. *Responses of two plant life-forms to low supplemental UV-B levels*

Analysis of the relatively low supplemental UV-B treatment studies revealed that the overall responses of herbaceous plants in total biomass (Bt, −7.0%, 95% CI [−11.7%, −2.1%], $N = 75$) and plant height (H, −4.8%, 95%CI [−7.3%, −2.3%], $N = 44$) to elevated UV-B radiation were significantly reduced (Fig. 1). Although the percentage changes of woody plants under this elevated UV-B level were greater than those of herbaceous plants, the negative effects on the two variables of woody plants were not significant. Also, effects of the low supplemental UV-B radiation on the other response variables of both life-forms, such as below- and above-ground biomass (Br and Bs), leaf biomass (Bl), leaf area (LA), root: shoot ratio (R/S) and specific leaf area (SLA), did not differ from zero.

In addition, under the low supplemental UV-B level, both life-forms demonstrably increased their UV-B-absorbing compound contents (Abs): woody plants exhibited a 15.6% increase (Fig. 2; 95% CI [3.0%, 29.7%], $N = 10$) and herbaceous plants showed a 10.8% increase (95% CI [6.2%, 15.6%], $N = 67$). Neither of the life-forms displayed significant changes in the chlorophyll a/b ratio (a/b) and total chlorophyll content (Chl). The chlorophyll a (Chla, −13.8%, 95% CI [−20.6%, −6.4%], $N = 25$), chlorophyll b content (Chlb, −16.3%, 95% CI [−28.7%, −1.7%], $N = 22$) and carotenoid content (Cm, −18.0%, 95% CI [−27.4%, −7.4%], $N = 20$) on a mass basis in herbaceous plants responded significantly to this elevated UV-B level. Moreover, the photosynthetic rate (Ph) of woody (−21.9%, 95% CI [−30.7%, −11.9%], $N = 16$) and herbaceous plants (−10.8%, 95% CI [−18.5%, −2.4%], $N = 24$) decreased significantly. The variation of photosynthetic rate under the low supplemental UV-B radiation did not differ significantly between the two life-forms ($Q_b = 3.44$, d.f. $= 1$, $P = 0.063$).

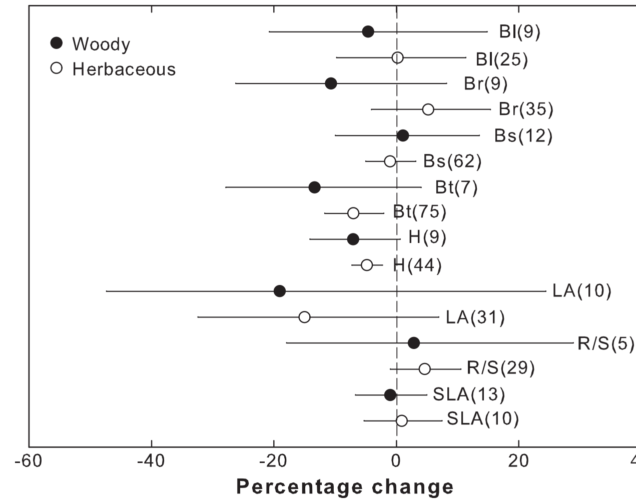

Fig. 1. Biomass and morphological responses of the two life-forms to the relatively low supplemental UV-B level (18–40% of ambient UV-B). Symbols represent percentage changes at the low supplemental UV-B radiation and the surrounding bars indicate the 95% confidence intervals (CIs). Observation numbers for each CI appear in parenthesis after the symbols.

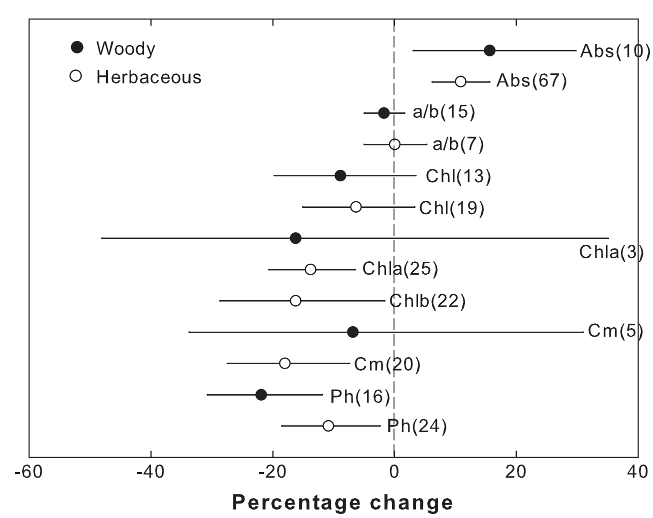

Fig. 2. Physiological responses of two life-forms under the relatively low supplemental UV-B level (18–40% of ambient UV-B). Symbols represent percentage changes at the low supplemental UV-B radiation and the surrounding bars indicate the 95% CIs. Observation numbers for each confidence interval appear in parenthesis after the symbols.

3.2. Responses of two plant life-forms to high supplemental UV-B levels

When exposed to supplemental UV-B levels that were more than 40% of ambient UV-B, woody plants (−13.6%, 95% CI [−24.8%, −0.8%], $N = 19$) and herbaceous plants (−11.7%, 95% CI [−17.6%, −5.4%], $N = 53$) both showed a negative effect on total biomass. In addition, the above-ground biomass (Bs) of herbaceous plants was reduced significantly (−16.6%, 95% CI [−22.2%, −10.7%], $N = 80$) (Fig. 3). Leaf areas of the two plant life-forms decreased (woody plants: −16.8%, 95% CI [−26.1%, −6.4%], $N = 13$; herbaceous plants: −16.1%, 95% CI [−20.4%, −11.6%], $N = 45$), though the difference between them was not significant ($Q_b = 0.02$, d.f. = 1, $P = 0.888$). Herbaceous plants exhibited reduced height (H, −11.1%, 95% CI [−14.3%, −7.7%], $N = 62$) and specific leaf area (SLA, −8.4%, 95% CI [−12.5%, −4.2%], $N = 37$) to a significantly greater extent upon exposure to the relatively high UV-B, as compared to the low supplemental UV-B (H, $Q_b = 5.52$, d.f. = 1, $P = 0.019$; SLA, $Q_b = 5.84$, d.f. = 1, $P = 0.016$). As compared to this, the changes in woody plant height ($Q_b = 0.24$, d.f. = 1, $P = 0.625$) and SLA ($Q_b = 0.37$, d.f. = 1, $P = 0.543$) did not significantly differ between the two elevated UV-B levels. Leaf area (LA) of both plant life-forms was significantly affected by the relatively high supplemental UV-B radiation.

The high supplemental UV-B treatment induced a significant effect on the UV-B-absorbing compound contents of both woody (15.0%, 95% CI [1.1%, 30.8%], $N = 25$) and herbaceous plants (37.0%, 95% CI [24.9%, 50.2%], $N = 49$) (Fig. 4). The increase of herbaceous UV-B-absorbing compounds was significantly greater than that observed under the low supplemental level ($Q_b = 11.29$, d.f. = 1, $P = 0.001$), while in woody plants, this variable did not differ significantly between the two UV-B levels ($Q_b = 0.01$, d.f. = 1, $P = 0.906$). Additionally, the Abs results under the higher UV-B level were different between the two life-forms ($Q_b = 5.11$, d.f. = 1, $P = 0.024$), despite the fact that the 95% CI slightly overlapped. The high supplemental UV-B level significantly affected total chlorophyll content (−12.7%, 95% CI [−16.7%, −8.6%], $N = 34$), chlorophyll a content (−12.3%, 95% CI [−22.9%, −0.06%], $N = 15$), chlorophyll b content (−16.4%, 95% CI [−24.9%, −6.9%], $N = 15$) and carotenoid content (−6.0%, 95% CI [−11.4%, −0.4%], $N = 26$) in herbaceous plants, but not in woody plants. Herbaceous photosynthetic rate (−20.1%, 95% CI [−26.8%, −12.8%], $N = 27$), which was restrained by the decrease of chlorophyll content, was significantly reduced under the high supplemental UV-B level. Only two data points were available for changes in the carotenoid content of woody plants; these showed increases of 2.2% and 4.0% under this UV-B level. Three data points (not shown in Fig. 4) were available for woody photosynthetic rate; they displayed conflicting trends (4.8%, 6.8%, and −10.5%, respectively) after exposure to this UV-B radiation level.

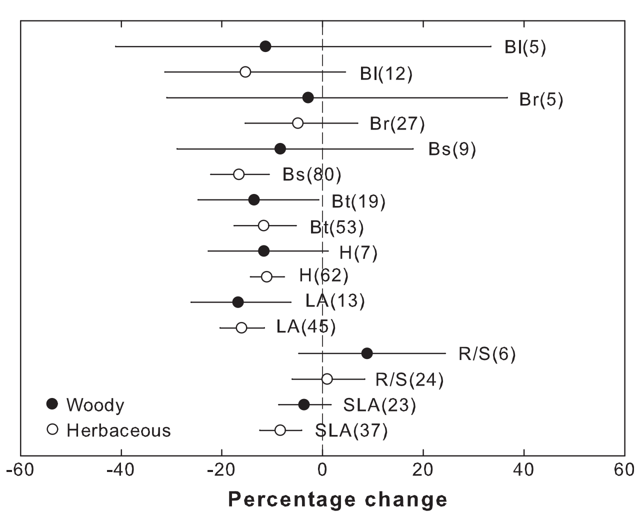

Fig. 3. Biomass and morphological responses of the two life-forms under the relatively high supplemental UV-B level (>40% of ambient UV-B). Symbols represent percentage changes at the high supplemental UV-B radiation and the surrounding bars show the 95% CIs. Observation numbers for each CI appear in parenthesis after the symbols.

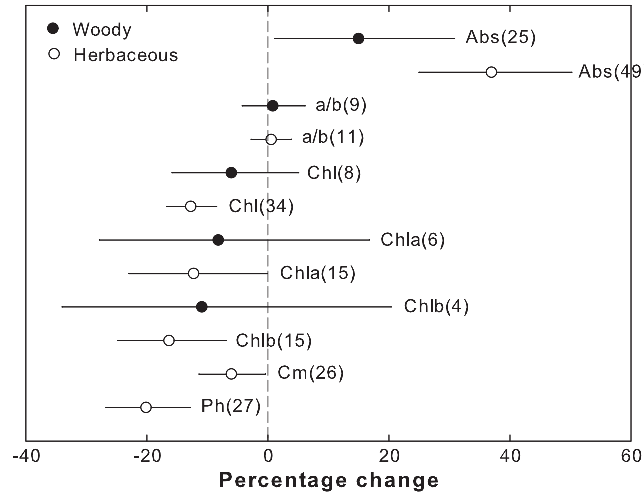

Fig. 4. Physiological responses of two life-forms under the relatively high supplemental UV-B level (>40% of ambient UV-B). Symbols represent percentage changes at the high supplemental UV-B radiation and the surrounding bars show the 95% CIs. Observation numbers for each CI appear in parenthesis after the symbols.

4. Discussion

In this study, we analyzed the overall responses of biomass accumulation, morphology and physiology of woody and herbaceous plants to elevated UV-B levels. Reduction in biomass accumulation due to UV-B exposure was found in several species (Nogués et al., 1998; Feng et al., 2003; Cechin et al., 2008), but not in all species (Fiscus and Booker, 1995; Rozema et al., 1997; Bassman et al., 2002). The meta-analysis of Searles et al. (2001) showed a significant decrease in shoot biomass of 16% for field studies simulating greater than 20% O_3 depletion (equivalent to the high supplemental UV-B level), while in our analysis the decreases under the same UV-B level in herbaceous and woody shoot biomass were 16.6% and 8.4%, respectively. The reduction in Bt accumulation, which indicated total plant biomass and not merely Bs in our study, represented total cumulative effects of damage or inhibited physiological function (Smith et al., 2000). Under the low elevated UV-B level, the detrimental effects were likely to depend on plant life-forms. That is, in herbaceous plants total biomass was significantly decreased, while the negative effect on woody plants was just near-significant. However, the two plant life-forms would both be apt to significantly suffer overall reduced biomass production under the high supplemental UV-B level. On the other hand, decreased plant height, leaf area and specific leaf area, which thickens leaves and causes them to closely overlap, could decrease sensitivity to UV-B radiation and increase the length of the UV-B screening pathway by reducing the amount of radiation intercepted by plants (Jansen et al., 1998; Smith et al., 2000; Kakani et al., 2003; Wang et al., 2007). In our analysis, negative responses were found for most of the morphological variables of the two life-forms under increased UV-B levels. If UV-B radiation continues rising from the low elevated level to the high elevated level, significantly greater decreases of herbaceous SLA and H are expected, whereas there would be no similar reductions in the two variables in woody plants between the two elevated UV-B levels. It may be suggested that herbaceous plants would be more sensitive and need to induce stronger self-defense mechanisms to protect themselves from the detrimental effects of high supplemental UV-B radiation.

UV-B-absorbing compounds, which accumulate to shield plants against harmful UV-B radiation by absorbing UV-B radiation, were one of the best-described and most effective self-protective responses of plants to UV-B radiation (Smith et al., 2000; Rozema et al., 2002; Kakani et al., 2004). In a previous meta-analysis, Searles et al. (2001) reported a 10% increase of the UV-absorbing compounds due to elevated UV-B radiation. Our analysis revealed the increase was 18.8% and 9.0% for woody and herbaceous plants respectively, in response to the low supplemental UV-B, while herbaceous UV-B-absorbing compounds increased by 37% under the high UV-B treatments. The increased production of herbaceous UV-B-absorbing compounds was significantly different between the two supplemental UV-B levels, while that of woody plants was not. To some extent, these results could be explained from a cost-benefit standpoint; under continuously elevated UV-B radiation, woody plants would not invest in large amounts of UV-B-absorbing compounds and relatively ineffective UV-B screeners, as foliage is only retained for one growing season (Day et al., 1992). In recent years, some UV-B studies found large increases in UV-B radiation were unlikely to have a negative effect on plant photosynthesis (Xiong and Day, 2001; Bassman et al., 2002; Robson et al., 2003; Rozema et al., 2005). Our analysis suggested that the two supplemental UV-B radiation levels had significant negative effects on the overall responses of herbaceous photosynthetic rate and most pigment content variables. Therefore, it may be premature to predict that enhanced UV-B levels would not be a threat to the photosynthetic competence of a vast number of plant species, as the effects were likely to depend on the life-form and the degree of UV-B radiation intensity.

Since plants were exposed to continuously varying UV-B levels, they may continuously adjust their UV defense mechanisms (Jansen et al., 1998). Nevertheless, the two plant life-forms showed different response strategies as UV-B radiation increased. Out of all the response variables that were analyzed, five variables for woody plants were significantly affected by UV-B radiation while sixteen variables for herbaceous plants were significantly affected. And the changes in herbaceous H, SLA and UV-B-absorbing compounds under the high elevated UV-B level were significantly greater compared with changes under the low supplemental UV-B level. To some extent, this suggested that different plant life-forms may have intrinsic capabilities to resist UV-B damage. Small herbaceous plants usually exhibit more rapid responses to environmental fluctuations than large woody species (Bradshaw and McNeilly, 1981; Rapport et al., 1985; Weng and Zhou, 2005), while woody plants possess perennial above-ground parts as well as steady plant structures and are in turn not as sensitive to shifting environmental conditions. Previous studies (Lin et al., 1998; Liang and Zhou, 2007) pointed out that the content of UV-B-absorbing compounds was generally higher in woody plants than herbaceous plants. Woody plants, especially conifer species, have a more effective UV-B screening mechanism, which may be an adaptive response to potentially large lifetime doses of UV-B radiation (Day et al., 1992). The UV-B-absorbing compounds of herbaceous plants are primarily located in the vacuoles of epidermal cells, while in woody plants they are present both in vacuoles and within epidermal cell walls (Schnabl et al., 1986; Schmelzer et al., 1988; Strack et al., 1989).

Differences between species in UV-B-induced changes in biomass, morphology and physiology may affect competitive interactions and ecosystem processes (Gehrke et al., 1995), as some species may out-compete others. Moreover, flavonoids and other phenolics are not only important for protection against UV-B radiation and oxidative stress, but also affect plant–herbivore, plant–pathogen and plant–symbiont interactions (Aphalo, 2003; Caldwell et al., 2003). Although we have no direct data about these interspecies relationships, it is likely that as UV-B radiation continues to increase, vegetation patterns will change and grassland ecosystems should be given more attention in future vegetation management.

Woody plants serving as canopy layers in natural ecosystems receive more sunlight and hence more UV-B radiation than herbaceous plants. As UV-B effects may be cumulative (Naidu et al., 1993) and woody plants are long-lived, the relatively small changes in productivity and/or morphology which were observed in currently available studies may result in some long-term effects. Some studies discussed the difficulties encountered in assessing the effects of enhanced UV-B on forest tree species (Bassman et al., 2002), and our analysis revealed that the attainable data for woody plants were notably less substantial than those for herbaceous plants. The overall responses of most woody plant variables to elevated UV-B radiation had very large confidence intervals. Perhaps the effect of elevated UV-B would vary with different woody types (such as conifer or broad-leaved trees, trees with or without N-fixing symbionts), which need to be evaluated with more independent studies about woody plants.

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