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Original article

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