

**Broadleaf and conifer tree responses to long-term enhanced UV-B radiation  
in outdoor experiments: a review**

Odziv listavcev in iglavcev na dogotrajno povečano obsevanje z UV-B v  
naravnih razmerah: pregledni članek

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**Abstract:** Trees as a perennial growth form require time to evolve the complex response to enhanced ultraviolet-B radiation (UV-B), and this might lead to slow but important changes in forest ecosystem structure and function. Long-term outdoor experiments on trees however are few in number. The available published results suggest that broadleaf and conifer trees may show different response strategies to enhanced UV-B radiation. The long-term outdoor experiments indicate species- and season-specific differential responses in tree secondary metabolism, photosynthesis, water relations, and growth and development.

**Keywords:** broadleaf tree, conifer tree, UV-B radiation, long-term outdoor experiment

**Izvleček:** Drevesa s svojo dolgoživo življenjsko obliko potrebujejo čas, da razvijajo kompleksen odziv na povečano ultravijolično-B (UV-B) sevanje, kar lahko vodi do počasnih a pomembnih sprememb v zgradbi in delovanju gozdnih ekosistemov. Kljub temu so dolgotrajni poskusi na drevesih izvedeni v naravnem okolju maloštevilni. Rezultati iz literature kažejo, da listavci in iglavci lahko uberejo različne strategije odzivanja na povečano sevanje UV-B. Dolgotrajni poskusi izvedeni v naravnih razmerah kažejo različne vrstno in sezonsko specifične odzive na nivoju sekundarnega metabolizma, fotosinteze, gospodarjenja z vodo ter rasti in razvoja dreves.

**Ključne besede:** listavci, iglavci, sevanje UV-B, večletni poskus, naravne razmere

## Introduction

Increases in solar ultraviolet-B radiation (UV-B) due to the continuing depletion of stratospheric ozone have been well documented over the past several decades (Madronich et al. 1998). A report from the World Meteorological Organization (WMO) estimates that full recovery

of stratospheric ozone on a global scale will not occur before 2050 – 2100 and will depend upon continued compliance with the Montreal Protocol. The magnitude, longevity and spatial variation of changes in ozone concentrations remain a matter of study. Additionally, a linkage between ozone depletion and global warming has been proposed because of stratospheric cooling which tends

toward ozone depletion reactions (WMO 2010).

The response of plants to UV-B radiation has gained attention over the past four decades. Most of the studies have involved agricultural and annual species, with fewer studies on trees. In spite of the importance of those woody plants in ecosystem productivity, function and in economics (Julkunen-Tiitto et al. 2005), studies on trees are relatively few.

Studies on the effects of UV-B radiation on plants have used artificial UV-B irradiation sources such as sunlamps. The spectral output of sunlamps varies moderately according to lamp type and supply function, which is either a square-wave or a modulated wave (Sullivan 2005). The dosage used for irradiation in different studies varied immensely (Aphalo et al. 2012). Some experiments have utilized filters to reduce natural solar UV-B radiation and studies utilizing filters are of interest because they do not modify the spectral balance between UV-B and UV-A and UV-B and PAR and do not account for the UV-C that must be filtered from artificial lamp systems. Such experiments are more practical in remote natural environments where electric power is unavailable. Readers interested in more detailed explanation of UV-B research treatments, lamps, and filters are referred to Aphalo and co-workers (2012) for the most current detailed analysis of UV-B methodology.

Due to logistical limitations, a majority of studies conducted on trees have been performed on seedlings, but some studies have also been conducted on large trees (Laakso and Huttunen 1998, Sullivan et al. 2003).

Our knowledge of UV-B effects on trees is based to some extent on short-term experiments, covering less than one season. The perennial growth form of trees and/or the presence of evergreen foliage in the conifers and evergreen broadleaf species require time to evolve the complex response which is observed over a longer period of UV-B irradiation. The presumed cumulative effect of long-term UV-B radiation will not be observable in short-time experiments (Mirecki and Teramura 1984, Laakso et al. 2000). Accordingly, the present review will focus on studies which were carried out through one season or longer (Table 1).

Some studies on the effects of UV-B radiation on plants have been carried out in growth chambers or greenhouses where the natural light

was limited and the artificial light failed to match, even closely, the intensity or spectral composition of natural light, specifically the ratio of UV-B to both UV-A and PAR (Sullivan 2005). The UV-B effect on plants in diminished and modulated light conditions is usually much more detrimental than is observed in studies of trees grown outdoors, where natural light conditions contribute to an effective tree response to UV-B (Laakso and Huttunen 1998). As a consequence, studies conducted in light conditions far from the natural solar light spectrum will not be considered in this review.

### UV-B effects on plants

In general, the responses of trees to UV-B radiation are assumed to be similar to those of other plants. The response of high altitude and southern latitude plants to UV-B radiation is often less pronounced than response of low altitude and northern latitude plants, which shows acclimation of first two plant groups to enhanced UV-B (Turunen and Latola 2005). Sensitivity of trees to UV-B is however species-specific (Rozema et al. 2002) and related to the perennial growth form of trees and/or evergreen foliage in conifers and evergreen species.

Early investigations considered UV-B radiation merely as an environmental stressor for plants causing cell damage (Björn et al. 1999), but more recently, UV-B radiation has come to be regarded also as a regulator of plant growth and development. UV-B radiation regulates the expression of numerous genes involved in diverse plant processes, including metabolism, photosynthesis, morphogenesis, and defence against pests and pathogens (Rozema et al. 2002, Brown et al. 2005). Many of these responses are triggered by UV-B, and this is consistent with the involvement of a UV-B photoreceptor, UVR8, which regulates a range of UV-B responses by controlling transcription of over a hundred genes (Favory et al. 2009, Rizzini et al. 2011).

Plants respond to harmful doses of UV-B radiation with defence and repair mechanisms, namely reflection by waxy surface structures and hairs, induction of secondary metabolites, and repair of biomolecules (Day et al. 1992, Day 1993, Karabourniotis et al. 1999, Keiller and Holmes

2001, Rozema et al. 2002). Secondary metabolites such as flavonoids and other phenolic compounds are important in plant tolerance of UV-B radiation as screens that reduce UV-B penetration into leaf tissue (UV-B absorbing compounds), and as antioxidants protecting the plants from damage by reactive oxygen species (Rozema et al. 2002, Sullivan 2005). Further studies will research interactions occurring at the threshold UV-B dose where regulation and stress-induced plant morphogenesis overlap (Robson et al. 2014).

### UV-B effects on trees

The first studies demonstrating UV-B effects on trees began in the 1970s and were conducted in greenhouses and growth chambers (Basioumy and Biggs 1975, Bogenrieder and Klein 1982). Sullivan (2005) reports that over 30 coniferous and broadleaf tree species were screened at that time and one-half of the conifers and one-third of the broadleaf species examined showed negative effects of exposure to supplemental UV-B radiation (Sullivan 2005). Subsequently, various valuable molecular approaches to studies of plant UV-B responses were developed. Among these there were a few long-term field studies on trees, and these offered additional insight into the complex response of trees to UV-B radiation and a natural condition of interactive environmental stresses (Trošt Sedej and Gaberščik 2008, Nybakken et al. 2012, Trošt Sedej and Rupar 2013, Virjamo et al. 2014).

Comparison of the responses of trees to UV-B radiation conducted on the same species in the field and in a greenhouse revealed that the responses were dominated by differences in experimental conditions. This article attempts to avoid the largest experimental variations by limiting further discussion to only long-term outdoor experiments.

#### *UV-B effects on broadleaf trees*

Enhanced UV-B radiation has been shown to induce various responses in broadleaf trees (Table 1). These range from morphological alterations to changes in biomass accumulation, physiology and metabolism (Kostina et al. 2001, Lavola et al. 2003, Sullivan 2005, Julkunen-Tiitto et al. 2005).

The most diverse response of broadleaf trees to enhanced UV-B radiation in long-term outdoor studies was observed in the rate of photosynthesis. This was found to decline in leaves of *Fraxinus excelsior*, *Betula pendula*, *Tilia cordata*, *Quercus robur*, and *Acer pseudoplatanus* after five years exposure to enhanced UV-B radiation (Keiller and Holmes 2001) and in *Fagus sylvatica* after three years exposure (Šprtova et al. 2003). Decrease in photosynthesis at multiple sites was attributed to direct UV-B damage to the photosynthetic apparatus, the oxygen evolving complex, D1/D2 reaction centre proteins, other components of photosystem II and Rubisco enzyme, as well as indirect damage through production of reactive oxygen species, reduced gas exchange by UV-B induction of stomatal closure and altered light environment within the leaf due to the changes of leaf anatomy (Nogues et al. 1999, Kataria et al. 2014). On the other hand, the lack of damage to photosynthesis in some broadleaf trees may be related to low penetration of UV-B through the epidermis (Day et al. 1992, Sullivan et al. 1996). The rate of photosynthesis was unaffected by exposure to enhanced UV-B radiation in *Quercus robur* after UV-B exposure for one year (Antonelli et al. 1998) and in *Liriodendron tulipifera* and *Liquidambar styraciflua* after three years (Sullivan et al. 2003). The potential photochemical efficiency was unchanged in *Fagus sylvatica* after three years of UV-B irradiation (Trošt Sedej and Rupar 2013). In *Acer rubrum* (Sullivan et al. 2003) the assimilation rate increased after three years of enhanced UV-B irradiation. It has been suggested that photosynthesis enhancement in *Acer rubrum* is due to increased levels of hydroxycinnamates in the mesophyll that could enhance blue light fluorescence induced by UV-B and contribute to carbon assimilation. Other researchers explained photosynthesis enhancement in terms of an increase in photosynthetic pigments (Warren et al. 2002).

In long-term outdoor studies, elevated UV-B radiation is found consistently to reduce a second, well-studied physiological parameter, transpiration. Transpiration was reduced in *Fraxinus excelsior*, *Betula pendula*, *Tilia cordata*, *Quercus robur*, and *Acer pseudoplatanus* after five years exposure to enhanced UV-B (Keiller and Holmes 2001) and in *Quercus rubrum*, *Liriodendron tulipifera* and *Liquidambar styraciflua* after three years of UV-B

exposure (Sullivan et al. 2003). UV-B radiation induces stomatal closure directly by inhibiting K<sup>+</sup> accumulation in the guard cell plasmalemma, so that the transpiration through stomata decreases (Nogués et al. 1999). Besides, stomatal density may increase whereas the aperture of stomata may decrease under enhanced UV-B radiation (Zu et al. 2010). In Mediterranean plants cuticle thickening was observed under enhanced UV-B radiation, which reduced cuticle transpiration during the dry Mediterranean summer (Manetas et al. 1997).

Studies suggested that under enhanced UV-B radiation, trees may suffer an overall negative effect in total biomass. Furthermore, UV-B affected biomass accumulation in trees can be expected to be observed over several growing seasons as the defence costs accumulate (Keski-Saari and Julkunen-Tiitto 2003, Trošt Sedej and Gaberšček 2008). Decreased biomass may be a result of a decrease in chlorophyll content, photosynthesis or leaf area under enhanced UV-B radiation, which has been well established in crop plants but not in trees (Laakso et al. 1996, Li et al. 2010). Enhanced UV-B radiation reduces growth, even when there is no decrease of photosynthesis, and thus may be a consequence of altered carbon allocation or changes in the canopy structure (Nogués et al. 1998) or perhaps altered phytohormones (Robson et al. 2014). A long-term UV-B study on broadleaf tree detected no effect on biomass accumulation in *Salix myrsinifolia* after two years irradiation (Nybakken et al. 2012).

Long-term outdoor studies on the morphological parameters of broadleaf trees commonly demonstrated alteration in leaf thickness and leaf area. The increase in leaf thickness decreases the penetration of UV-B radiation to the photosynthetic leaf tissue. Leaf thickness increased with elevated UV-B radiation in *Quercus robur* (Antonelli et al. 1998) and in *Betula pendula* (Kostina et al. 2001), and leaf area was found to decrease in *Fraxinus excelsior*, *Betula pendula*, *Tilia cordata*, *Quercus robur* and *Acer pseudoplatanus* after five years exposure to enhanced UV-B radiation (Keiller and Holmes 2001), and in *Acer rubrum* and *Liliodendron tulipifera* after three years exposure (Sullivan et al. 2003). In contrast, leaf area in *Betula pendula* after one year of enhanced UV-B irradiation was not affected (Kostina et al. 2001) and was even increased in *Liquidambar styraciflua* after three

years of enhanced UV-B irradiation (Sullivan et al. 2003). The mechanisms of leaf area reduction were not clarified but it appears that they are not necessarily the result of damage to the photosynthetic mechanism, because they do not always correlate with decrease in photosynthesis.

Trees contain a wide variety of different phenolic compounds, the bioactive components which are species-, genotype- and tissue-specific. They are present in leaves, stems, buds, flowers and roots, although their quantity and composition change in the course of plant development (Rozema et al. 2002). UV-B radiation has been shown to increase the accumulation of several secondary phenolic compounds under certain environmental conditions in some species. Flavonoids in particular and other phenolic compounds absorb strongly in the UV-B range (UV-B absorbing compounds) and also act as antioxidants scavenging reactive oxygen species (Tevini and Teramura 1989, Teramura and Sullivan 1994). The accumulation of UV-B absorbing compounds in the epidermis was shown to reduce UV-B radiation transmittance to deeper photosynthetic leaf tissues thus protecting sensitive targets (Caldwell et al. 1998).

The total UV-B absorbing compounds increased in *Quercus robur* after one year of UV-B exposure (Antonelli et al. 1998), in *Liriodendron tulipifera* after three years of UV-B exposure (Sullivan et al. 2003) and in *Salix myrsinifolia* after two years of UV-B exposure (Nybakken et al. 2012). Other studies demonstrated unchanged levels of total UV-B absorbing compounds in broadleaf trees after long-term UV-B irradiation, such as in *Quercus rubra* (Warren et al. 2002), *Acer rubrum* and *Liquidambar styraciflua* (Sullivan et al. 2003) and *Fagus sylvatica* (Trošt Sedej and Rupar 2013). The accumulation of UV-B absorbing compounds is dependent upon many environmental factors and in addition to UV-B protection, it may also impact plant-insect interactions in a variety of ways (Sullivan 2005).

#### *UV-B effects on conifer trees*

The most studied response of conifer trees to enhanced UV-B concerns phenolic compounds in their role as UV-B absorbing compounds (Table 2). Many studies have demonstrated that the epidermis of fully grown needles of conifers contains high

Table 1: Long-term (1 year or more) field UV-B studies on broadleaf trees. Significant tree response is marked with: + (positive), - (negative), o (insignificant)

Tabela 1: Dolgotrajni UV-B poskusi na listavcih v naravnih razmerah. Statistično značilen odziv drevesa je označen kot: + (pozitiven), - (negativen), o (neznačilen)

Broadleaf tree	Exposure (years)	Treatment	Plant response	Authors	
<i>Quercus robur</i>	1	UV-B	Photosynthesis	o	Antonelli et al. 1998
			<b>UV-B absorbing compounds</b>	+	
			<b>Leaf thickness</b>	+	
<i>Betula pendula</i>	1	UV-B	Leaf area	o	Kostina et al. 2001
			<b>Leaf thickness</b>	+	
<i>Acer pseudoplatanus</i>	5	UV-B	<b>Photosynthesis</b>	-	Keiller and Holmes 2001
<i>Betula pendula</i>			<b>Transpiration</b>	-	
<i>Fraxinus excelsior</i>			<b>Leaf area</b>	-	
<i>Quercus robur</i>					
<i>Tilia cordata</i>					
<i>Quercus rubra</i>	3	UV-B	UV-B absorbing compounds	o	Warren et al. 2002
<i>Acer rubrum</i>	3	UV-B	<b>Photosynthesis</b>	+	Sullivan et al. 2003
			<b>Transpiration</b>	-	
			UV-B absorbing compounds	o	
			<b>Leaf area</b>	-	
<i>Liquidambar styraciflua</i>	3	UV-B	<b>Photosynthesis</b>	o	Sullivan et al. 2003
			<b>Transpiration</b>	-	
			UV-B absorbing compounds	o	
			<b>Leaf area</b>	+	
<i>Liriodendron tulipifera</i>	3	UV-B	Photosynthesis	o	Sullivan et al. 2003
			<b>Transpiration</b>	-	
			<b>UV-B absorbing compounds</b>	+	
			<b>Leaf area</b>	-	
<i>Fagus sylvatica</i>	3	UV-B	<b>Photosynthesis</b>	-	Šprtová et al. 2003
<i>Fagus sylvatica</i>	3	UV-B	Fv/Fm	o	Trošt Sedej and Rupar 2013
			Chlorophylls	o	
			UV-B absorbing compounds	o	
<i>Salix myrsinifolia</i>	2	UV-B	Biomass	o	Nybakken et al. 2012
			<b>UV-B absorbing compounds</b>	+	
		↑T	<b>Biomass</b>	+	
		UV-B x ↑T	<b>UV-B absorbing compounds</b>	-	
			<b>Biomass</b>	++	
	<b>UV-B absorbing compounds</b>	+			

amounts of phenolic compounds which can prevent the penetration of potentially detrimental UV-B radiation to the photosynthetic tissue below (Day et al. 1992, DeLucia et al. 1992). UV-B absorbing compounds are located both in vacuoles and within epidermal cell walls (Fischbach et al. 1999, Hoque and Remus 1999; Rozema et al. 2002, Turtola et al. 2006). The effective UV-B screening mechanism is an acclimation response to UV-B radiation and a significant part of a protective strategy of plants (Day et al. 1992, DeLucia et al. 1992, Trošt Sedej

and Gaberščik 2008). Important component of the defence systems against enhanced UV-B is reflectance of UV light (Hoque and Remus 1999), special anatomical characteristics of the epidermis (Hoque and Remus 1999, Chalker-Scott and Scot 2004), and large amounts of different secondary compounds which, acting as antioxidants scavenge reactive oxygen species (Turtola et al. 2006).

Even though the accumulation of UV-B absorbing compounds is an acclimation response to solar UV-B that varies over spatial (latitude, altitude,

canopy) and temporal (season, day) scales, phenolic compounds in conifers mostly do not respond to enhanced UV-B radiation in long-term outdoor experiments. Thus, UV-B absorbing compounds

failed to respond to enhanced UV-B in *Pinus pinea* and *Pinus halepensis* after one year of irradiation and drought (Petropoulou et al. 1995), in *Pinus ponderosa* and *Pseudotsuga menziesii* after three

Table 2: Long-term (1 year or more) field UV-B studies on conifer trees. Significant tree response is marked with: + (positive), - (negative), o (insignificant)

Tabela 2: Dolgotrajni UV-B poskusi na iglavcih v naravnih razmerah. Statistično značilen odziv drevesa je označen kot: + (pozitiven), - (negativen), o (neznačilen)

Conifer tree	Exposure (years)	Treatment	Plant response	Authors
<i>Pinus taeda</i>	3	UV-B	<b>Biomass</b>	- Sullivan and Teramura 1992
<i>Pinus taeda</i>	3	UV-B	<b>Fv/Fm</b> <b>Biomass</b>	- Naidu et al. 1993 -
<i>Pinus halepensis</i> <i>Pinus pinea</i>	1	UV-B x drought	<b>Fv/Fm</b> <b>Photosynthesis</b> Chlorophylls UV-B absorbing compounds	+ Petropoulou et al. 1995 o o
<i>Pinus taeda</i>	1	UV-B	<b>Biomass</b>	- Sullivan et al. 1996
<i>Pinus pinea</i>	1	UV-B	Fv/Fm Biomass	o Manetas et al. 1997 o
	1	UV-B x drought	<b>Fv/Fm</b> <b>Biomass</b>	+ +
<i>Picea abies</i>	2	UV-B	<b>Photosynthesis</b> <b>Chlorophylls</b>	- Šprtova et al. 1999 -
<i>Pinus sylvestris</i>	3	UV-B	<b>UV-B absorbing compounds</b>	- Kinnunen et al. 2001
<i>Pinus ponderosa</i> <i>Pseudotsuga menziesii</i>	3	UV-B	UV-B absorbing compounds	o Warren et al. 2002
<i>Picea abies</i>	1	UV-B	Chlorophylls	- Kirchgessner et al. 2003
<i>Picea abies</i>	5	UV-B	Fv/Fm Photosynthesis Chlorophylls UV-B absorbing compounds Biomass <b>Branch diameter</b> <b>Fv/Fm</b>	o Trošt Sedej and o Gaberščik 2008 o o o - +
	5	UV-B x drought	Photosynthesis Chlorophylls UV-B absorbing compounds Biomass	o o o o
<i>Picea abies</i>	1	UV-B	UV-B absorbing compounds Biomass	o Virjamo et al. 2014 o
	1	UV-B x ↑T	<b>UV-B absorbing compounds</b> Biomass	+ o
	1	UV-B x ↑T x fertilization	<b>UV-B absorbing compounds</b> Biomass	+ o

years of irradiation (Warren et al. 2002) and in *Picea abies* after five and one years of irradiation (Trošt Sedej and Gaberščik 2008, Virjamo et al. 2014). These last two studies also demonstrated that UV-B absorbing compounds increased in *Picea abies* when UV-B radiation was combined with other environmental stresses such as drought, high temperature and fertilizer. The UV-B absorbing compounds synthesis partly correlated with the needle age class (Trošt and Gaberščik 2008). The amount of UV-B absorbing compounds in *Pinus sylvestris* decreased after three years of enhanced UV-B radiation, which may indicate an inadequacy of the protective mechanisms when faced with an accumulated UV-B dose (Kinnunen et al. 2001).

High accumulation of UV-B absorbing compounds in the epidermis of many conifer trees results in low penetration of UV-B through the epidermis and absence of damage to the photosynthesis (Day et al. 1992, Sullivan et al. 1996, Fischbach et al. 1999; Hoque and Remus 1999, Turtola et al. 2006). This may also be the case in *Pinus pinea* after one year of enhanced UV-B irradiation and *Picea abies* after one/five years (Manetas et al. 1997, Trošt Sedej and Gaberščik 2008). The last two conifer species, *Pinus halepensis* and *Pinus pinea* (Petropoulou et al. 1995) even demonstrated an increase in photochemical efficiency under the interactive effect of enhanced UV-B combined with drought. This may be a result of an increase in leaf thickness and consequently, a decrease of UV-B penetration into mesophyll as well as a restriction in cuticular transpiration (Manetas et al. 1997). Decline in photosynthesis, which may be due to UV-B induced damage to the photosynthetic apparatus or to UV-B induction of stomatal closure or to altered light environment within the leaf, was observed in *Pinus teada* and *Picea abies* after three and two years of enhanced UV-B radiation, respectively. In *Picea abies* the decrease in photosynthesis could be correlated with the decrease in chlorophyll content (Naidu et al. 1993, Šprtova et al. 1999). Studies have reported negative, neutral and occasionally, positive effects of enhanced UV-B radiation on chlorophyll content (Bassman et al. 2003, Kirchgessner et al. 2003, Lavola et al. 2003, Trošt Sedej and Gaberščik 2008, Láposi et al. 2009). It was shown that UV-B radiation can not only inhibit chlorophyll synthesis or cause photo-oxidation of chlorophyll

(Bornman 1989, Middleton and Teramura 1993), as was observed in *Picea abies* (Šprtova et al. 1999, Kirchgessner et al. 2003) but under favourable irradiation conditions, it can also increase the biosynthesis of photosynthetic pigments (Middleton and Teramura 1993, Jordan 1996) although this has not been confirmed in any long-term field experiment. There was no significant impact on chlorophyll content in *Pinus halepensis* and *Pinus pinea* after one year or in *Picea abies* after five years of enhanced UV-B radiation (Petropoulou et al. 1995, Trošt Sedej and Gaberščik 2008).

The UV-B susceptibility of biomass accumulation in conifer species proved to be in *Pinus taeda*, where biomass decreased after one year (Sullivan et al. 1996) as well as after three years of enhanced UV-B irradiation (Sullivan and Teramura 1992, Naidu et al. 1993). In *Picea abies* no effect on biomass was detectable after either one and five years of enhanced UV-B irradiation or after interaction of UV-B, drought, high temperature and fertilization exposure (Trošt Sedej and Gaberščik 2008, Virjamo et al. 2014). Meanwhile, in *Pinus pinea* biomass accumulation was not affected by UV-B, while an alleviating effect of enhanced UV-B to biomass was observed during drought (Manetas et al. 1997).

## Conclusion

The diversity of results in different studies reflects the complex response of trees to UV-B radiation as a function of a wide spectrum of environmental factors and their multilevel interactions. The levels of UV-B absorbing compounds in broadleaf trees increase frequently after enhanced UV-B radiation which is not the case in conifer trees which however may benefit more of constitutive flavonoid synthesis. Even though the responses are species-specific; there is no clear general agreement concerning the response of broadleaf and conifer trees to enhanced UV-B radiation.

## Summary

The response of plants to UV-B radiation has attracted attention over the past four decades. Early investigations considered UV-B radiation to

be merely an environmental stressor causing cell damage in plants, but more recently, UV-B radiation has also been regarded as a possible regulator of plant growth and development. In this review, in order to avoid the largest experimental variations, we discuss long-term UV-B studies conducted on broadleaf and conifer trees in natural light conditions, with the aim of gaining some insight into the complex cumulative response of perennial plants.

In long-term outdoor studies in broadleaf trees, elevated UV-B radiation rather diversely affects photosynthetic rate, showing no effect on biomass accumulation but increasing leaf thickness in some cases. The UV-B absorbing compounds in the broadleaf tree either increased or were unchanged.

In conifer trees the most studied response to enhanced UV-B radiation was synthesis of UV-B absorbing compounds, which generally did not react to UV-B irradiation in long-term outdoor experiments. High accumulation of UV-B absorbing compounds in the epidermis of many conifer trees results in low penetration of UV-B through the epidermis and lack of damage to the photosynthetic mechanisms. The UV-B susceptible biomass accumulation in conifer species was observed in loblolly pine, but in other conifers, no effect on biomass was detected. In some conifers an alleviating effect of enhanced UV-B to biomass was observed during drought.

## Povzetek

Raziskave učinkov povečanega sevanja UV-B na rastline so se razmahnile tekom zadnjih štirih desetletij. V prvih raziskavah so sevanje UV-B smatrali predvsem kot stresni dejavnik, ki povzroča poškodbe celic, kasnejše raziskave sevanje UV-B obravnavajo tudi kot pomemben regulator rasti in razvoja rastlin. V tem preglednem članku povzemamo samo rezultate dolgotrajnih študij sevanja UV-B na listavcih in iglavcih izvedenih v naravnem okolju, z namenom izogniti se velikim eksperimentalnim razlikam in s ciljem poglobiti vpogled v kompleksni odziv dolgoživih rastlin na povečano sevanje UV-B.

Pri listavcih je povečano sevanje UV-B precej različno vplivalo na intenziteto fotosinteze, medtem ko učinka na kopičenje biomase ni bilo, vendar pa je pogosto prišlo do povečane debeline listov. UV-B absorbirajoče snovi so se povečale ali ostale nespremenjene.

Pri iglavcih so bile najbolj raziskane UV-B absorbirajoče snovi, ki se večinoma niso odzvale na povečano sevanje UV-B. Velike količine konstitutivnih UV-B absorbirajočih snovi so bile prisotne v povrhnjici mnogih iglavcev, kar je preprečilo prodiranje UV-B do fotosinteznih aktivnih tkiv lista in s tem tudi poškodb fotosinteznih procesov. Biomasa se pod vplivom povečanega sevanja UV-B ni spremenila, razen pri eni vrsti. Pri nekaterih iglavcih je ob sočasnem delovanju povečanega sevanja UV-B in suše prišlo do blaženja negativnih posledic sevanja.

Raznolikost rezultatov v študijah potrjuje kompleksnost kot tudi vrstno specifičnost odziva listnatih in iglastih dreves na povečano UV-B sevanje v odvisnosti od celotnega spektra okoljskih dejavnikov in njihovih interakcij.

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