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Seasonal Changes in UV-B Absorption in Beech Leaves (*Fagus sylvatica L.*) along an Elevation Gradient

Jahreszeitliche Veränderung der UV-B Absorption in Buchenblättern entlang eines Höhengradienten

By MECHTHILD NEITZKE and ALMUT THERBURG

Summary

Sun and shade leaves of beech (*Fagus sylvatica* L.) were collected along an elevation gradient in the Hunsrück region of Rhineland-Palatinate from May to September, 1999. Leaf area, specific leaf weight and concentration of UV-absorbing compounds (measured as UV absorption of methanolic extracts) were determined. At 280 and 320 nm, sun leaves exhibited higher absorptions per unit leaf area than shade leaves. For all three sampling times, a positive correlation was found between the absorption of UV-B radiation of shade leaves and the sampling site elevation. A positive correlation was also found between the absorption of sun leaves and the elevation for the samplings done in July and September. In addition, there was a positive correlation between the absorption of sun leaves from 290 to 400 nm and the sum of the index values indicating daily maximum UV radiation during the growing season. At all elevations between May and July, the sun leaves exhibited a sharp increase in absorption at 280 and 320 nm. From July to September no further increase could be observed. The shade leaves exhibited an increase in absorption at 280 and 320 nm throughout the growing season from May to September.

Keywords: *Fagus sylvatica*, UV-B absorption, elevation gradient, UV index, sun leaves, shade leaves.

Zusammenfassung

Entlang eines Höhengradienten im Hunsrück (Rheinland-Pfalz) wurden von Mai bis September Sonnen- und Schattenblätter der Rotbuche (*Fagus sylvatica* L.) gesammelt. Es wurden die Blattfläche, das spezifische Blattgewicht und der Gehalt an UV-Strahlung absorbierenden Verbindungen (gemessen als UV Absorption methanolischer Blattextrakte) gemessen. Sowohl bei 280 nm als auch bei 320 nm zeigten die Sonnenblätter eine höhere Absorption pro Blattfläche als die Schattenblätter. An allen drei Erntezeitpunkten wurde bei den Schattenblättern eine positive Korrelation zwischen der Absorption im UV-Bereich und der Höhenlage der beprobten Bäume gefunden, bei den Sonnenblättern nur für die Probenahmen im Juli und September. Darüber hinaus trat bei den Sonnenblättern eine positive Korrelation zwischen der Absorption in dem Wellenlängenbereich von 290 bis 400 nm und der Summe der täglichen Maxima der UV-Indices während der Wachstumsperiode auf. Die Sonnenblätter zeigten in allen Höhenlagen zwischen Mai und Juli einen starken Absorptionsanstieg zwischen 280 und 320 nm. Von Juli bis September konnte keine weitere Absorptionszunahme beobachtet werden. Die Schattenblätter zeigten dagegen eine Zunahme der Absorption bei 280 nm und 320 nm während der gesamten Vegetationsperiode von Mai bis September.

Schlüsselwörter: *Fagus sylvatica*, UV-B Absorption, Höhengradient, UV-Index, Sonnenblätter, Schattenblätter.

1 Introduction

Since 1977, a global depletion of the stratospheric ozone layer has been observed, manifested most strikingly by the so-called “ozone hole” which forms each year over Antarctica during the spring season in the southern hemisphere. The ozone column over the northern hemisphere has also been diminishing for many years with a corresponding increase in UV radiation as a result of reduced absorption by stratospheric ozone (KERR and MCELROY 1993, SECKMEYER et al. 1994, BOJKOV and FIOLETOV 1995, ZEREFOS et al. 1995, HERMAN et al. 1996, HARRIS et al. 1997, ZEREFOS et al. 1997). It is estimated that in the middle latitudes of the northern hemisphere (30−60° N), in comparison to values for the 1970's, erythema-effective UV radiation has increased by 7% for winter and spring, and by 4% for summer and fall (MADRONICH et al. 1998).

Most of the UV radiation which penetrates cells is absorbed and triggers serious damage due to its high quantum energy (e.g. BORNMAN 1989, CALDWELL et al. 1989, ROZEMA et al. 1997). Numerous studies have documented the negative impact of UV-B radiation on plants. In terms of morphology, a reduction in leaf and bud growth has been observed (e.g. GOLD and CALDWELL 1983). Chloroplasts seem to be particularly sensitive to UV-B radiation (e.g. BORNMAN 1989). On a molecular level, effects on nucleic acids, proteins, lipids, photosynthesis pigments and phytohormones have been observed (e.g. ROZEMA et al. 1997). Such effects are described in detail in a number of papers (CEN and BORNMAN 1990, BORNMAN and VOGELMANN 1991, BORNMAN and TEAMURA 1993, CALDWELL and FLINT 1994, HE et al. 1994, CALDWELL et al. 1995, FISCUS and BOOKER 1995, BARNES et al. 1996, CAASI-LIT et al. 1997, KRIZEK et al. 1997, ORMROD et al. 1997, JANSEN et al. 1998). Plants have evolved various mechanisms which can serve to counteract the potentially harmful effects of solar UV-B radiation. These mechanisms range from molecular, biochemical and physiological changes at the cellular level to morphological modifications of the entire plant (PANTEN et al. 1996). One of the most frequently occurring reactions is the synthesis of phenylpropanoid pigments which absorb UV-B radiation (ROBBERECHT and CALDWELL 1983, FLINT et al. 1985, BORNMAN and VOGELMANN 1988, 1991, TEVINI and TERAMURA 1989, LOVELOCK et al 1992, CEN and BORNMAN 1993, MIDDELTON and TERAMURA 1993, WILSON and GREENBERG 1993, YANG et al. 1995, ADAMSE and BRITZ 1996, RUHLAND and DAY 1996, KRAUSS et al. 1997, SCHNITZLER et al. 1997, OLSSON et al. 1999). However, the absolute amounts of constitutive and UV-B induced flavonoids vary greatly from species to species (BOHM 1987). Although these compounds have other important functions in plants, serving as flower coloration agents (HARBORNE 1967), anti-herbivore agents (MCCLURE 1976) and scavengers of free radicals (HUSAIN et al. 1987), flavonoids in leaf tissue can serve as a significant UV filter due to the UV absorption properties of these compounds (ROBBERCHT and CALDWELL 1983). Reflectance (approximately 10−20%) is generally lower in the UV-B region of the spectrum than in the visible region (ROBBERECHT et al. 1980). Flavonoids convert the absorbed UV radiation into heat in such a way that harmful photoreactions are not initiated in other molecules (RICHTER 1996). The importance of these pigments in protecting plants from the effects of UV-B radiation has been documented in various studies (e.g. CALDWELL et al. 1983, Li et al. 1993, DAY et al. 1994, JORDAN 1996, GRAMMATIKOPOULOS et al. 1999, OLSSON et al. 1999, MAZZA et al. 2000).

These UV-B screening pigments exhibit a high degree of compartmentalization in leaf tissue (SCHNABL et al. 1986, WEISSENBÖCK et al. 1986, SCHMELZER et al. 1988, STRACK et al. 1988,1989, DAY et al. 1992, 1993, DAY 1993, SCHNITZLER, et al. 1996, HUTZLER et al. 1998). While flavonoid and hydroxycinnamic acid metabolites usually accumulate in the central vacuoles of guard cells and epidermal cells as well as in the subepidermal cells of leaves, some compounds are covalently linked to plant cell walls and others occur in waxes (SCHMUTZ et al. 1994) or on the external surfaces of plant organs (CUADRA and HARBORNE 1996, CHAVES et al. 1997). Cell wall constituents and cuticular waxes are, in general, relatively transparent to UV and visible radiation (CROOKS 1978, FREY-WYSSLING 1976, WUHRMANN-MEYER and WUHRMANN-MEYER 1941). Measurements of the transmission of UV radiation in enzymatically isolated cuticular membranes have shown that transmission can vary from 0.03 to 50%. This corresponds to an attenuation factor of 2 to 4000 (RAU 1999). Although the attenuation is partly due to reflection of the incident radiation, the primary cause lies in absorption by corresponding pigments. Investigations of epidermal absorption of UV radiation have revealed considerable differences among various plant groups (DAY et al. 1992). While conifers exhibit an absorption of up to 100%, in the case of many herbaceous dicots, 40% of the UV-B radiation is still detectable in the mesophyll. Experiments with flavonoid-deficient mutants have clearly demonstrated the protective function of these substances (Li et al. 1993, Lois and Buchanan 1994, Stapelton and Walbot 1994, Mazza et al. 2000).

However, the synthesis of phenylpropanes is influenced not only by a multitude of site factors, such as high PAR or UV radiation (Chappell and Halbrock 1984, Wellmann 1985, Beggs and Wellmann 1994, Dixon and Pavia 1995), but also by the developmental stage of the plants (Popovici and Weissenböck 1976, Blume and McClure 1979, Peters 1987, Reuber 1991, Liu et al. 1995, Estiarte et al. 1999, Burchard 2001). Seasonal variations in the production of phenolic compounds have been reported for a variety of plants (Strack et al. 1989, Delucia et al. 1992, Mole and Joern 1993, Lois 1994, Nikolopoulos et al. 1995, Day et al. 1996, Vogt and Gölz 1996, Chaves et al. 1997, Heller et al. 1998, Fischbach et al. 1999). However, Dillenburg et al. (1995) found no significant effect on the concentration of UV-B absorbing compounds in leaves of seedlings of *Liquidambar styraciflua* L. at any stage of leaf growth. Delucia et al. (1992) and Day et al. (1996) postulate that the accumulation of flavonoids with increasing leaf age increases the effectiveness of UV-B absorption. Low concentrations of these compounds in young leaves may help to explain findings suggesting that younger foliar leaves are less effective in screening radiation and are more sensitive to increases in UV-B radiation (Delucia et al. 1992, Naidu et al. 1993).

Radiation regulation frequently occurs at the transcription level (Schmelzer et al. 1988, Strid 1993, Brosch et al. 1999), where various photoreceptors are involved which affect the gene expression either alone (Beggs et al. 1987) or operating together in a synergistic manner (Ohl et al. 1989, Jenkins 1997). The influence of UV radiation on the initial enzyme PAL and on the CHS enzyme (Kubasek et. al. 1992, Wu and Hahlbrock 1992, Haussühl et al. 1996, Kalbin et al. 1997), as well as on an increased accumulation of phenylpropanes, has been demonstrated in many investigations (Beggs and Wellmann 1985, Frohnmeyer et al. 1992, Lois 1994).

Most studies of the effect of increased UV-B radiation on plants involve experiments in climatic chambers, in greenhouses or in the field, using equipment which artificially irradiates the plants. Although forest ecosystems play a central role in the global carbon cycle, they are somewhat under-represented in studies of the effects of increased UV-B radiation. Reasons for this include the size of the trees and the vertical distribution of their leaves (McLeod and Newsham 1997). However, because of the significance of the forests, the question of the adaptability of various tree species to increasing UV-B radiation is particularly important. The majority of studies have focused on evergreen conifers (Kaufmann 1978, Kossuth and Biggs 1981, Sullivan and Teramura 1988, 1989, 1992, Fernbach and Mohr 1992, Stewart and Hoddinott 1993). Studies of conifers and angiosperms, conducted both in the greenhouse and in the field, demonstrate substantial growth and physiological responses to enhanced UV radiation in several species (Sullivan and Teramura 1988, 1992, Naidu et al. 1993, Delucia et al. 1994, Sullivan et al. 1994, 1996, Dillenburg et al. 1995, Schumaker et al. 1997, Nagel et al. 1998). Tree species exhibit a wide range of leaf anatomical characteristics, some of which could provide protection from enhanced UV-B radiation to a greater or lesser extent (Yang et al. 1995, Nagel et al. 1998).

In the present study, changes in the absorption of methanolic leaf extracts in the beech *Fagus sylvatica* L., one of the most common tree species in central Europe, are investigated along an elevation gradient. The reactions of species along natural UV-B radiation gradients can be used as an indicator of the ability to adapt to increasing stress from UV-B radiation (Caldwell et al. 1983). In the Alps, Blumthaler et al. (1997) observed an increase in UV radiation with altitude and also found that the altitude effect was clearly wavelength-dependent. For global radiation, the altitude effect was found to be 9 % per 1000 m for a wavelength of 370 nm, increasing gradually to 11 % per 1000 m for a wavelength of 320 nm. In the UV-B region of the spectrum, the altitude effect for global radiation increased markedly to 24% per 1000 m for a wavelength of 300 nm. The altitude effect for 280 nm is not reported, but it could be expected to be even more pronounced.

In recent years the formation of flavonoid pigments as a reaction to UV-B radiation has also been demonstrated for the beech. From methanolic extracts of beech leaves, HELLER et al. (1998) were able to isolate and identify more than 10 different UV-B absorbing secondary metabolites, which were soluble or bound to the cell wall. For some of these compounds a UV-B dependent accumulation was demonstrated. The localization of protective pigments in the leaf tissue with the aid of laser scanning microscopy showed a distinct accumulation of pigments in the epidermis. Over the course of the year both a development-related decrease (in the case of non-acylated, dissolved kaempferol gylcosides) and increase (in the case of soluble diacylated kaempferol derivates and kaempferol glycosides bound to the cell wall) in the various protective pigments could be observed. The composition of the waxes of the cuticle was also modified as a result of UV-B radiation during development (RAU 1999).

LIEGEL (1999) demonstrated that the gene expression of beech seedlings was modified by UV-B radiation. While some new gene products were present following UV-B exposure, others could no longer be detected. The fact that certain gene products appear for the first time under the influence of UV-B radiation, or are greatly increased, indicates that proteins are involved which lead to or contribute to an adaptation of the plant (RAU 1999).

In this study, changes in the UV-B absorption of beech leaves over the course of the growing season are of particular interest, since a relatively high level of UV-B stress on the leaves is to be expected in the spring after leaf emergence due to the greater depletion of the ozone column in the spring. Low concentrations of UV-B absorbing compounds in young leaves can result in young leaves less effectively protected from harmful UV-B radiation, causing them to react much more sensitively to an increase in UV-B radiation (DELUCIA et al. 1992, DAY et al. 1996, ESTIARTE et al. 1999).

In contrast to previously published investigations of beeches in which the effects of UV-B radiation have been studied by means of experimental manipulation using lamps or filters, in the present study the variation of UV-B radiation along an elevation gradient is used. Whereas in the studies of HELLER et al. (1998) the influences of UV-B radiation and leaf development on the absorption of UV-B radiation were investigated separately, the present study focuses on the combination of seasonally-determined variations in UV-B absorption and variations in the intensity of UV-B radiation along a natural elevation gradient.

Differences in the sensitivity of different tree species to an increase in UV-B radiation could lead to changes in the competitive situation and hence to changes in the distribution of species or the composition of forest ecosystems. It is hoped that this study will contribute to the evaluation of the reaction of forest ecosystems to a further increase in UV-B radiation at the earth's surface.

2 Materials and methods

The Hunsrück region, situated in the Schiefergebirge on the left bank of the Rhine, was selected as the research area because here the copper beech (*Fagus sylvatica* L.) is found growing along an elevation gradient over geologically very uniform parent rock. Here the Hunsrück slate and Taunus quarzite bedrock weather to form shallow, non-calcareous, nutrient-poor soils. The elevation gradient extends from 131 m above sea level in Trier to 816 m above sea level on the Erbeskopf mountain. The difference in elevation thus amounts to 685 m. The 1st sampling was carried out from late April to early May, 1999 (shortly after the emergence of the beech leaves), the 2nd from July 26 to August 9, 1999, and the 3rd from September 13 to 21, 1999. All of the leaves collected at each sampling time were approximately the same age. Since the leaves of plants along an elevation or climate gradient emerge at different times, the sampling times for the different elevations were staggered. Phenological observations of snowdrops (*Galanthus nivalis*) and apple blossoms in the Hunsrück region were used as a basis for timing the collection of samples at different elevations. There were 13 sampling sites along the elevation gradient (Fig. 1).

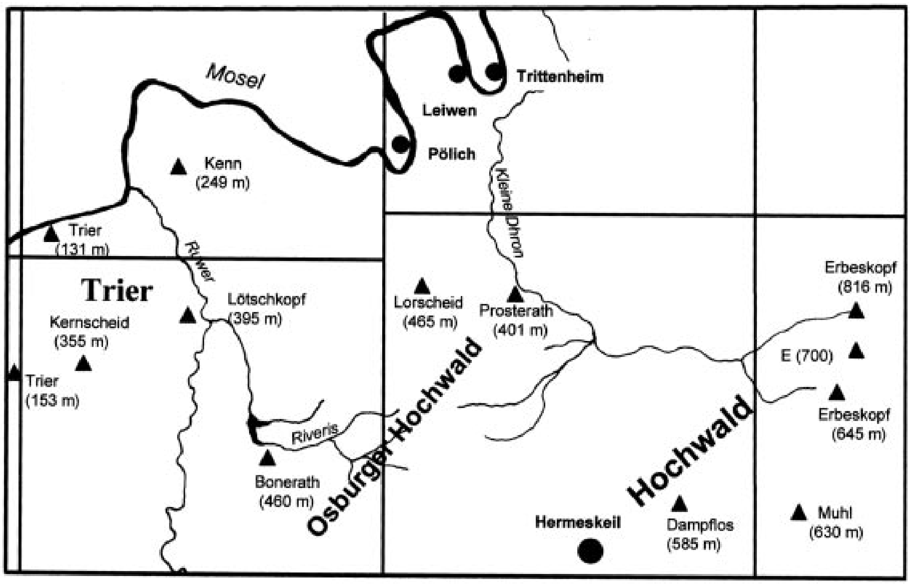

Fig. 1. Location of the study sites along an elevation gradient in the Hunsrück region (Germany).
Abb. 1. Lage der Probenahmestellen entlang eines Höhengradienten im Hunsrück (Deutschland).

Sampling was carried out using telescopic shears to cut beech twigs at heights of up to 10 m along wood margins with a south or southwest exposure. In the selection of leaves, sun leaves were distinguished from shade leaves. The sun leaves were all taken from the outermost leaf layer, which was fully exposed to solar radiation. It is assumed that the amount of radiation received by these leaves is comparable to that received by the outer leaves in the upper tree crown. At each sampling site, 3 twigs with sun leaves and 3 twigs with shade leaves were collected from each of 5 beeches which were standing adjacent to one another. The twigs were placed in polyethylene bags and transported in a cooler to the laboratory, where they were stored in a refrigerator (for a maximum of 24 h) until processed. Five healthy leaves were cut from each twig. For each of these leaves, the leaf area, fresh weight and dry weight were determined. A combined sample was prepared by combining and crushing the 15 sun leaves (or shade leaves) of a particular tree.

In accordance with the procedure employed by WAND (1995), measurements of UV-B absorbing substances were carried out using methanolic leaf extracts with a UV/visible spectrophotometer (Shimadzu UV-160a). For each sample, an extract was prepared using 20 mg dried, crushed plant material and 20 ml methanol, water and HCl (79:20:1, v/v/v).

The absorption spectrum was measured at 280, 290, 300, 310 and 320 nm, and for selected samples was also measured in 5-nm increments for wavelengths from 200 to 400 nm. This method permits differences in UV absorption to be determined even when the substances involved in the absorption are unknown.

The global solar UV index was used as an indicator of the stress from solar UV-B radiation along the transect. Values for this index, which is a measure of the solar UV radiation at the earth's surface that is relevant for human erythema, have been forecast by the German Weather Service since 1997. The values are defined for a horizontal surface and are reported as the daily maximum of erythema-effective UV radiation. The global solar UV index is internationally standardized and values for this index are forecast in many countries, including most European countries, America, Australia and New Zealand. In Europe, UV index values vary from 0 as a minimum to 10 in the summer, at Gibraltar. The maximum value of the UV index is approximately 6 in northern Germany, 7 in southern Germany and more than 8 in the Alps. These forecasts are based on 1) satellite measurements of total ozone (TOVS), 2) the 48-hour forecast of changes in total ozone due to changes in temperature developing at altitudes of 3 to 25 km, 3) the amount of solar UV radiation reaching the earth's surface, as calculated using the STAR (System for Transfer of Atmospheric Radiation) spectral model of the University of Munich, assuming cloudless skies, taking into account the expected stratification of temperatures and assuming the slight to medium continental aerosols representative of German summer conditions, and 4) adjustment of the erythema-effective UV radiation forecast for cloudless skies to take into account forecast cloud conditions in the low, middle and high cloud layers, using an empirical 5-step scale. The index values are calculated as the integral of the erythema-effective UV intensity for the spectral range of 290 to 400 nm. Conversion to W_{ery} m^{-2} can be effected by dividing the UV index value by 40 (Jendritzky et al. 1997). German Weather Service forecasts are based on a grid system, with grid cells measuring approximately 14 × 14 km. The study transect in the Trier/Hunsrück region is covered by five grid cells (Fig. 1). The UV index values forecast for a particular cell are based on the average elevation of that cell. For the purpose of this study, these values were adjusted to reflect the actual elevations of the sampling sites according to the formula that for an increase in altitude of 1000 m, the UV index value increases by 7.5 % (Jendritzky et al. 1997).

Since damage from UV-B radiation is presumed to be a function of the cumulative dose (Sisson and Caldwell 1976, Sisson and Caldwell 1977, Tevini and Teramura 1989, Day et al. 1996), for each sampling site the maximum UV index values for each day were added together from the time of assumed leaf emergence to the time of sampling. These cumulative values were correlated with the area beneath the absorption curve from 290 to 400 nm.

Statistical analyses were performed by means of SPSS, using Spearman's rank correlations and nonparametric tests [Mann-Whitney and Kruskal-Wallis (Sachs 1984)].

3 Results

3.1 Leaf parameters

As expected, significant differences were found between sun and shade leaves in terms of leaf area, dry weight and specific leaf mass (Table 1). For all of the sampling times, the average leaf area of the shade leaves was 10 cm^2 larger than that of the sun leaves (5 % level of significance). Whereas there was no difference in leaf area for the different sampling times, the dry weight and hence also the specific leaf mass increased sharply between the 1st sampling in May and the 2nd sampling in July (0.1 % level of significance). Because of the difference in the increase in leaf thickness, the increase in dry weight between the 1st and 2nd samplings was considerably less for the shade leaves than for the sun leaves. Over the course of the growing season the moisture content of the shade leaves decreased from approximately 70 % relative to the fresh weight to 50–60 %. In the sun leaves the decrease was considerably more pronounced, with the result that in July and August the moisture content of the sun leaves was less than that of the shade leaves; the difference was statistically significant. In only three cases was there a correlation between the growth parameters of the sun and shade leaves and the elevation of the sampling site (Table 2).

Table 1. Growth parameters of sun and shade leaves of beech (*Fagus sylvatica* L.) (mean of all leaves per sampling time (n=975) and standard deviation, significant differences between sun and shade leaves are indicated by capitals and between different sampling times by small letters).

Tabelle 1. Wachstumsparameter von Sonnen- und Schattenblättern der Buche (*Fagus sylvatica* L.) Mittelwerte aller pro Probenahmezeitpuntk geernteten Blätter (n = 975) und Standardabweichung, signifikante Unterschiede zwischen Sonnen- und Schattenblättern sind durch Großbuchstaben und zwischen verschiedenen Probenahmezeitpunkten durch kleine Buchstaben gekennzeichnet).

	Sun leaves			Shade leaves		
	May	**July**	**September**	**May**	**July**	**September**
Leaf area (cm^2)	**23.7**^{Aa} ± 4.2	**21.2**^{Aa} ± 3.0	**22.2**^{Aa} ± 2.7	**30.2**^{Ba} ± 6.0	**31.4**^{Ba} ± 4.7	**31.5**^{Ba} ± 3.6
Leaf dry weight (mg)	**111.3**^{Aa} ± 36.2	**194.4**^{Ab} ± 24.2	**174.5**^{Ab} ± 28.6	**72.8**^{Ba} ± 18.6	**104.1**^{Bb} ± 26.1	**114.7**^{Bb} ± 13.8
Water content (%)	**69.5**^{Aa} ± 4.0	**49.5**^{Ab} ± 1.3	**51.6**^{Ab} ± 1.8	**71.7**^{Aa} ± 3.6	**59.9**^{Bb} ± 3.8	**59.1**^{Ab} ± 2.8
Specific leaf mass (mg · cm^{-2})	**4.5**^{Aa} ± 0.9	**9.2**^{Ab} ± 0.7	**8.2**^{Ab} ± 0.8	**2.3**^{Ba} ± 0.3	**3.3**^{Bb} ± 0.6	**3.6**^{Bb} ± 0.6

Table 2. Spearman's rank correlations for the correlation between some growth parameters of sun and shade leaves of beech (*Fagus sylvatica* L.) and the elevations of the sampling sites (* 5%; ** 1%).

Tabelle 2. Korrelationskoeffizienten für die Beziehungen zwischen einigen Blattparametern von Sonnen- und Schattenblättern der Buche (*Fagus sylvatica* L.) und der Höhenlage der Probenahmestellen (* 5%, ** 1%).

	Sun leaves			Shade leaves		
	May	**July**	**September**	**May**	**July**	**September**
Leaf dry weight (mg)	−0.339	−0.148	0.151	−0.167	−0.111	−0.211
Leaf area (cm^2)	0.031	−0.131	0.037	−0.102	−0.473	−0.606*
Water content (%)	0.186	−0.691**	0.351	0.047	−0.609*	0.145
Specific leaf mass (mg · cm^{-2})	−0.208	0.02	−0.149	0.402	0.184	0.299

3.2 UV absorption spectra

3.2.1 Seasonal Changes

For all three sampling times, the absorption of methanolic extracts of sun leaves differed considerably from that of shade leaves, not only in terms of the level of absorption in the UV-B region of the spectrum, but also in terms of absorption patterns in the range of wavelengths from 200 to 400 nm.

The concentration of UV-B absorbing compounds on the basis of leaf area increased with leaf age (Fig. 2, Fig. 3). For the 1st sampling, in the spring, the absorption spectra of both the sun and shade leaves exhibited a clearly defined absorption maximum only at around 220 nm (225 nm for sun leaves and approximately 210 nm for shade leaves) (Fig. 2). From 250 to 400 nm a slight, continuous decrease in absorption was recorded. Throughout the whole range of wavelengths the absorption of the shade leaves was lower than that of the sun leaves. Over the course of the growing season the absorption spectra of the sun leaves changed in a characteristic manner. In July and September, in addition to an increase in absorption over the whole range of UV wavelengths, a second, much smaller absorption maximum was recorded between 280 and 285 nm (Fig. 2). In the case of the shade leaves this peak at around 280 nm (the second peak) was much lower as was

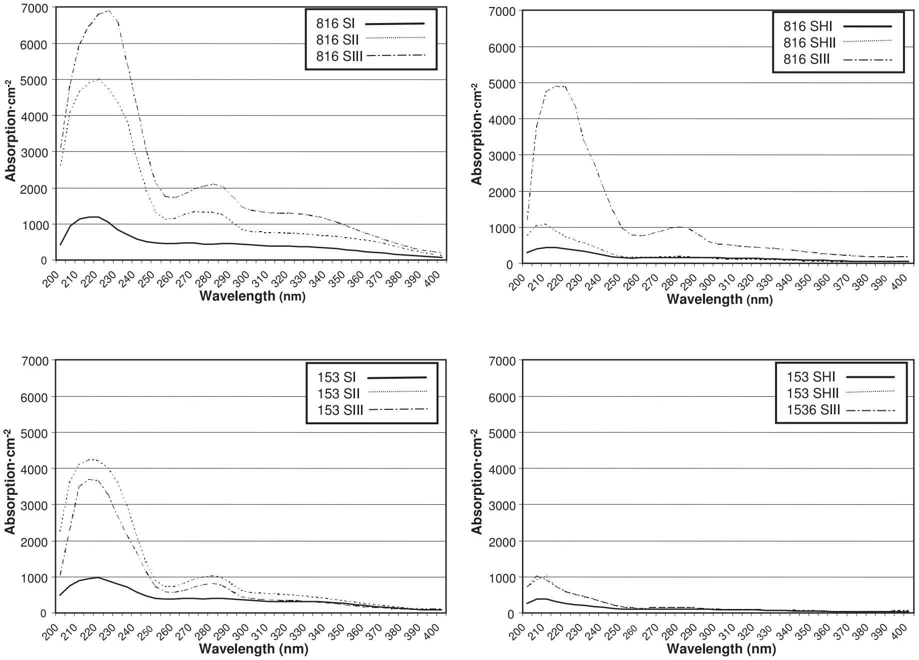

Fig. 2. Changes in the absorption in the UV region of the spectrum of sun (S) and shade (SH) leaves of *Fagus sylvatica* in 153 m and 816 m in the course of the vegetation period (I: May, II: July, III: September).

Abb. 2. Veränderung der Absorption im UV-Bereich bei Sonnen (S)- und Schattenblättern (SH) der Buche (*Fagus sylvatica* L.) in 153 m und 816 m ü. NN im Verlauf der Vegetationsperiode (I: Mai, II: Juli, III: September).

the level of absorption for the remaining range of wavelengths. In the case of the sun leaves, the sharpest increase in absorption in the UV-B region of the spectrum was recorded for the period from May to late July/early August (Fig. 3). By September no further increase had occurred. In contrast, in the case of the shade leaves, absorption in the UV-B region of the spectrum continued to increase to the time of the last sampling, in September (Fig. 3). However, the increase in absorption was considerably less in the case of the shade leaves than in the case of the sun leaves. Whereas the increase in absorption at 280 nm averaged 300 % for the sun leaves, the increase for the shade leaves was between 50 and 100 %.

3.2.2 Elevational Changes

In the case of the sun leaves, the values of the two maxima (220–225 nm and 280–285 nm) increased markedly with increasing elevation of the sampling site above sea level. In the case of the shade leaves, the increase was only slightly pronounced (Fig. 4). The absorption in the UV-B region was represented by absorption at the wavelengths 280 and 320 nm since these constitute the upper and lower boundaries of the UV-B region of the spectrum. However, for the 1st sampling in May a statistically significant correlation between the elevation of the sampling sites and the absorption at 280 and 320 nm was found only for the shade leaves (Table 3). In contrast, for the 2nd and 3rd samplings there were highly significant positive correlations between the absorption at the two wavelengths 280 and 320 nm and the elevation of the sampling sites above sea level for both the sun and shade leaves (Table 3, Fig. 5). At both 280 and 320 nm the absorption of the sun

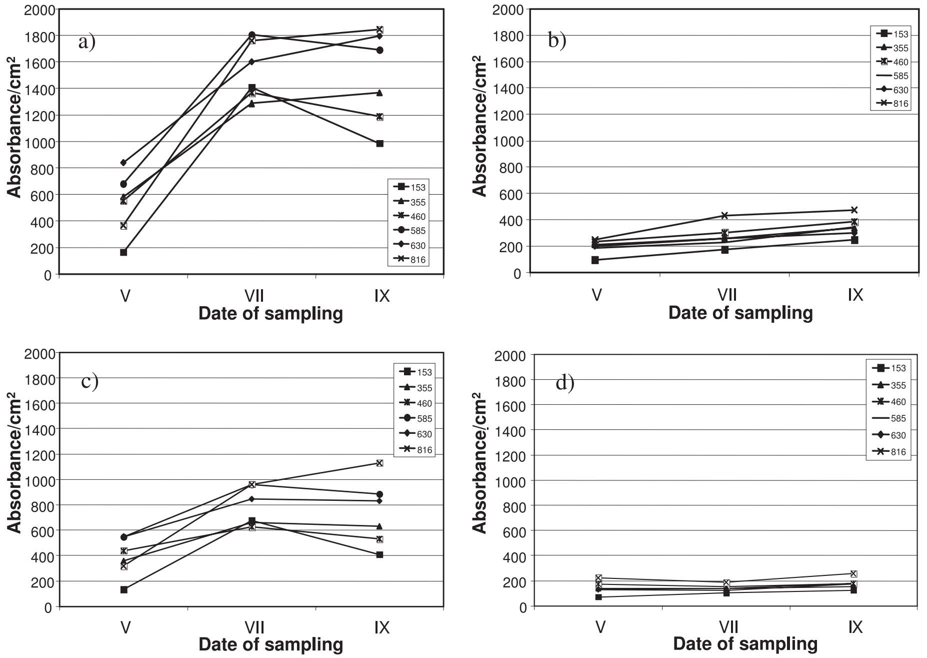

Fig. 3. Changes in the absorption at 280 nm and 320 nm of sun and shade leaves of *Fagus sylvatica* from May to September (V: May, VII: July, IX: September) along an elevation gradient (a): sun leaves at 280 nm; b): shade leaves at 280 nm; c): sun leaves at 320 nm, d): shade leaves at 320 nm). Only 6 of 13 sampling points are shown.

Abb. 3. Veränderung der Absorption bei 280 nm und 320 nm von Sonnen- und Schattenblättern der Buche (*Fagus sylvatica* L) von Mai bis September (V: Mai, VII: Juli, IX: September) entlang eines Höhengradienten (a): Sonnenblätter bei 280 nm, b): Schattenblätter bei 280 nm, c): Sonnenblätter bei 320 nm, d): Schattenblätter bei 320 nm). Dargestellt sind nur 6 von 13 Probenahmestellen.

leaves approximately doubled with the 685-meter increase in altitude along the elevation gradient. However, the absorption between 290 and 400 nm (calculated from the area beneath the absorption curve for the range of wavelengths from 290 to 400 nm) also increased along the elevation gradient. A highly significant correlation was also found between the absorption from 290 to 400 nm and the sum of the daily maximum UV index values during the growing season (Fig. 6).

4 Discussion and Conclusion

Beech (*Fagus sylvatica* L.), one of the most common deciduous tree species in central Europe, is distributed over a wide range of elevations (0−1500 m) and latitudes (from southern Sweden to Sicily) and hence occurs along natural UV-B radiation gradients (Oberdorfer 1983). Over the course of its development from seedling to mature tree the stress from UV-B radiation can also change markedly. Whereas the development of seedlings takes place predominantly in the half-shade of the parent trees, the crowns of the mature trees are exposed to high radiation intensities depending on the stand density. Brown et al. (1994) found that under closed canopies 40−70% of the incident UV-B radiation was absorbed by the top 25% of the canopy. In addition, within each tree there is a steep UV-B radiation gradient depending on the exposure of the leaves (sun and shade leaves). The fact that individual leaves as well as entire trees are found along natural

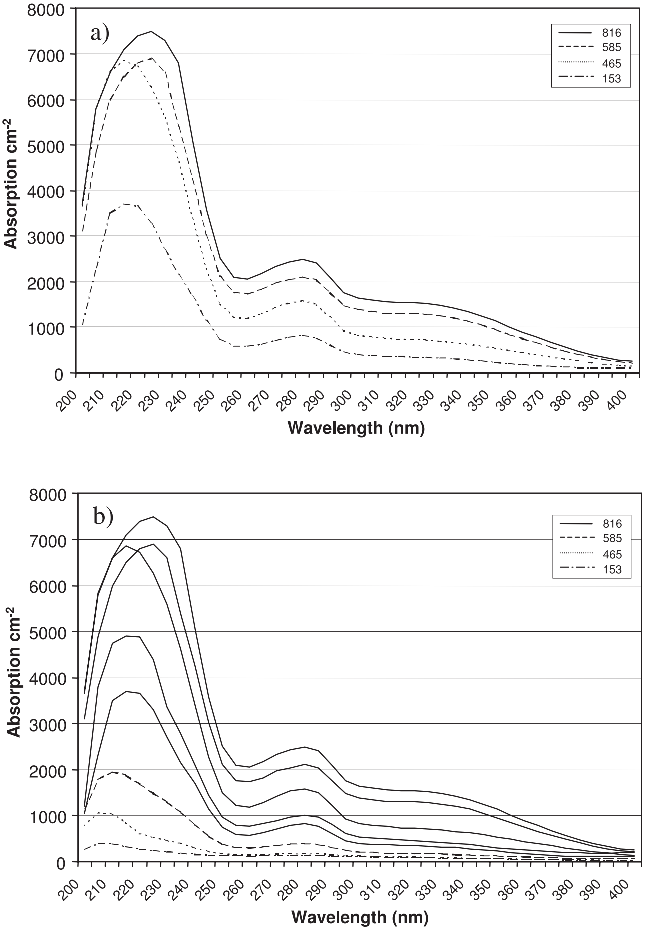

Fig. 4. Absorption of sun (a) and shade (b) leaves of *Fagus sylvatica* in the UV region of the spectrum in 153 m, 465 m, 585 m and 816 m in September.

Abb. 4. Absorption von Sonnen (a) und Schattenblättern (b) der Buche (*Fagus sylvatica* L.) im UV-Bereich in 153 m, 465 m, 585 m und 816 m ü. NN im September.

UV-B radiation gradients suggests a good adaptation of beech to changing UV-B radiation conditions. Comparative studies of the adaptation of various genera to natural UV-B radiation gradients resulting from variations in elevation and latitude have been carried out by Robberecht et al. (1980) and Lavola (1998) among others. With one exception (Neitzke and Therburg 2000) such studies are not available for beech.

In comparison with evergreen species (Day et al. 1993, Karabourniotis et al. 1995), relatively few studies have been carried out which examine the developmental and seasonal variations in the concentration of UV-B absorbing substances in the leaves of deciduous trees (Antonelli et al. 1998, Dillenburg et al. 1995, Heller et al. 1998). Considering its importance beech is also under-represented here. The same applies to long-term studies. Although several studies have been carried out which compare sun and shade leaves with regard to the effects of radiation on biochemical and anatomical features that influence UV-B screening effectiveness (Warner and Caldwell 1983, Mirecki and Teramura 1984, Cen and Bornman 1990, Lovelock et al. 1992, Adamse et al. 1994), there is a lack of

Table 3. SPARMAN's rank correlations for the correlation between the absorption of methanolic extracts of sun and shade leaves of beech (*Fagus sylvatica* L.) and the elevation of the sampling sites in the course of the vegetation period 1999 (* 5 %; ** 1 %; *** 0,1 %).

Tabelle 3. Korrelationskoeffizienten für die Beziehung zwischen der Absorption methanolischer Blattextrakte von Sonnen- und Schattenblättern der Buche (*Fagus sylvatica* L.) und der Höhenlage der untersuchten Buchen im Verlauf der Vegetationsperiode 1999 (* 5 %; ** 1 %; *** 0.1 %).

	Sun leaves			Shade leaves		
	May	**July**	**September**	**May**	**July**	**September**
Absorption · cm^{-2}$_{(280\ nm)}$	0.324	0.645*	0.824***	0.697**	0.622*	0.736**
Absorption · cm^{-2}$_{(320\ nm)}$	0.450	0.640*	0.774**	0.663*	0.649*	0.779**
Absorption · g^{-1}$_{(280\ nm)}$	0.240	0.640*	0.811***	0.595*	0.706**	0.797**
Absorption · g^{-1}$_{(320\ nm)}$	0.500	0.747**	0.743**	0.255	0.669*	0.840***

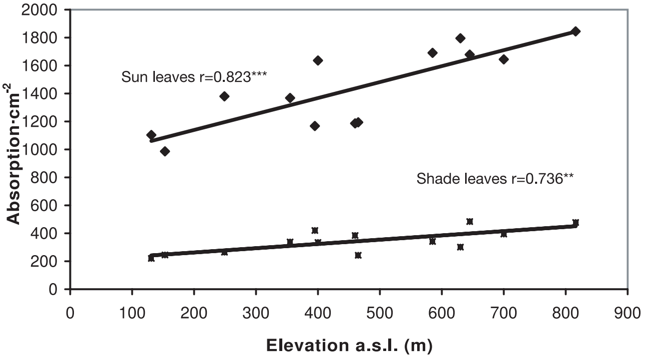

Fig. 5. Absorbance per leaf area of methanolic extracts of sun and shade leaves of *Fagus sylvatica* L. at 280 nm plot as a function of the elevation of the sampling points in the Hunsrück.

Abb. 5. Absorption methanolischer Blattextrakte von Sonnen- und Schattenblättern der Buche (*Fagus sylvatica* L.) bei 280 nm in Abhängigkeit von der Höhenlage (m ü. NN) der Probenahmepunkte im Hunsrück.

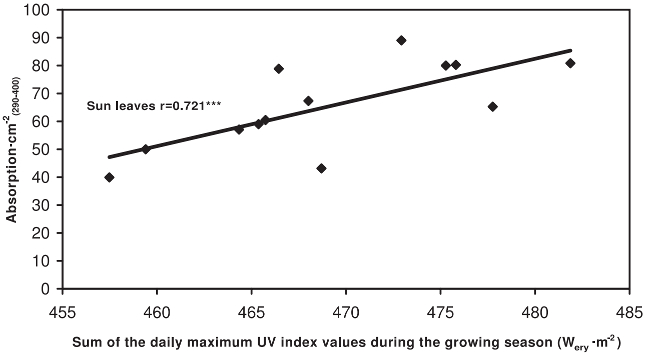

Fig. 6. Absorbance between 290 and 400 nm of methanolic extracts of sun leaves of *Fagus sylvatica*nd in July plot as a function of the sum of the daily maximum UV index values during the growing season at the different sampling points along an elevation gradient in the Hunsrück.

Abb. 6. Beziehung zwischen der Absorption methanolischer Extrakte von Sonnenblättern der Buche (*Fagus sylvatica* L.) im Wellenlängenbereich zwischen 290 und 400 nm im Juli und der Summe der täglichen maximalen Werte des UV-Indexes während der Wachstumsperiode an den verschiedenen Probenahmestellen entlang eines Höhengradienten im Hunsrück.

investigations which compare variations in the concentration of UV-B absorbing substances in sun and shade leaves over the course of the year.

The present study makes use of a natural UV-B radiation gradient along an elevation gradient. It should be kept in mind that field investigations have certain disadvantages as compared to investigations using greenhouses or climatic chambers. Among these is the high degree of variability of environmental factors and biological material. In order to take this variability into account a large number of samples was used in comparison with the number of samples required for other types of investigation. Another disadvantage of field investigations is the delay in processing the samples due to the time required to transport the samples to the laboratory. No empirical evidence is available concerning the effect of cooled storage on the concentrations of UV-B absorbing compounds. However, it is known that concentrations in dried materials are subject to very little change to the extent that herbarium materials are used as bioindicators of UV-B radiation conditions in the past (MARKHAM et al. 1990, BJÖRN et al. 1997). It should also be noted that samples taken from wood margins with a southern exposure are subject to a different angle of radiation than would be the case at the outer edges of the tree crowns. However, in the case of UV, and particularly UV-B radiation, 40 to 75 % of the radiation occurs in the isotropic diffuse component, which substantially reduces the effect of leaf inclination (CALDWELL 1981). While field studies have certain disadvantages, they avoid some of the problems associated with climatic chamber and greenhouse studies, such as insufficient PPFD and an unrealistically low PPFD/UV-B.

In this investigation, an adaptation of beech leaves to their UV-B radiation environment was observed over the course of the growing season. The concentration of UV-B absorbing compounds increased not only with increasing leaf age and hence increasing duration of UV-B exposure, but also with increasing UV-B stress along an elevation gradient. The increase in UV-B radiation absorption with both increasing leaf age and increasing UV-B radiation along an elevation gradient was modified by the position of the leaves on the tree, as is strikingly illustrated by the differences between the sun and shade leaves.

An increase in UV-B absorbing compounds with increasing leaf age in the sun leaves of beech was also observed in studies by HELLER et al. (1998). These researchers, who also carried out a determination of the protective pigments of beech, found an increase in soluble diacylated kaempferol derivatives, particularly the cell wall-associated kaempferol glycosides, over the course of the growing season from May to September.

The increase in absorption in the UV-B region of the spectrum over the course of the growing season can be attributed to developmental variations as well as to an induction of UV-B absorbing compounds by environmental factors. HELLER et al. (1998) found evidence for both processes in the sun leaves of beech.

Higher concentrations of UV-B absorbing compounds could result in greater UV-B screening effectiveness with increasing leaf age. The limited UV-B absorption in young leaves could mean that in the early stages of development, in May, effective shielding from harmful UV-B radiation by the epidermis or outer leaf layers is not yet possible with the result that at this time the leaves have an increased sensitivity to UV-B radiation. This is particularly significant in view of the fact that recent predictions based on stratospheric chemistry and climate-change models estimate that in northern areas (60–90 ° N) the maximum springtime UV-B radiation will increase by as much as 50–60 % in the years 2010 to 2020, as compared with long-term means (SHINDELL et al. 1998, TAALAS et al. 2000). It was found that the increase in UV-B absorption in sun leaves over the course of the growing season followed a saturation curve. It is conceivable that beech leaves have only a limited capacity for synthesizing protective pigments, which for the sun leaves was already completely exhausted by July, and that for this reason no further increase in the synthesis of UV-B absorbing substances was possible even with an increased duration of radiation exposure.

The age-dependent variations of concentrations of UV-B absorbing compounds appear to be species-specific. Thus some deciduous trees (*Betula pendula* and *Betula resinifera*) exhibit an increase in UV-B absorbing compounds with increasing leaf age (Lavola 1998), while in other species (*Liquidambar styraciflua*) no age-dependent variations have been observed (Dillenburg et al. 1998, Sullivan et al. 1996).

Differences between the absorption patterns of sun and shade leaves in the UV region of the spectrum have also been documented in the literature for other plant species (Larcher 1984, McDougal and Parks 1986, Lovelock et al. 1992, Liakoura et al. 1997). Since sun leaves are exposed to higher levels of UV and visible radiation than shade leaves (Caldwell et al. 1983), the higher absorption in the UV-B region of the spectrum may contribute to the protection of the sun leaves from UV radiation. Investigations by Heller et al. (1998), in which an induction of UV-B absorbing compounds by UV-B radiation was shown, make it seem very probable that the observed differences in the absorption behavior of sun and shade leaves were caused by differences in exposure to UV-B radiation. In the case of the shade leaves the capacity for synthesizing UV-B absorbing compounds in the radiation conditions prevailing in the interior of the tree crown did not appear to be exhausted, as shown by the fact that the absorption, in contrast to that of the sun leaves, continued to increase steadily until September.

In the case of both sun and shade leaves, the UV-B absorption increased with increasing sampling site elevation. Whereas in sun leaves absorption in the UV-B region of the spectrum reached a plateau in July, it continued to increase in shade leaves. The level of the saturation curve plateau increased with increasing sampling site elevation. There were statistically highly significant correlations between sampling site elevation and absorption in the UV-B region of the spectrum. It is to be assumed that with increasing radiation intensity at higher elevations higher concentrations of UV-B radiation absorbing compounds were synthesized. For sun leaves of beech Heller et al. (1998) demonstrated a dependence of the accumulation of UV-B and UV-A absorbing metabolites on UV-B radiation. The presence of a UV-B radiation gradient along the study transect was confirmed by surveys of the Department of Climatology of the University of Trier (personal communication). Since at the time of the investigations a weather or meteorological station did not exist on the Erbeskopf mountain, it was not possible to assess the influence of cloud cover on the radiation conditions. This also applies to possible effects of weather on the radiation received by the leaves, which could have arisen due to the staggering of the sampling times. Since due to inversion weather conditions valley fog occurred much more frequently than high-level fog along the study transect, the occurrence of fog probably did not displace the radiation gradient (i.e. lower influence of radiation in the valley than at high elevations).

As the evaluation of the surveys of the Department of Climatology has not yet been completed, the values for erythemal-effective radiation forecast as a UV index by the German Weather Service were used as an indication of the increase of UV-B radiation along the elevation gradient of the study transect. Here a close correlation between the UV index values and the absorption of methanolic leaf extracts in the UV region from 290 to 400 nm was also found. For the beech leaves these observations suggest a connection between absorption in the UV-B region of the spectrum and the intensity of the UV-B radiation and duration of exposure.

Although a correlation between the level of UV-B absorption and sampling site elevation was found for shade leaves for the 1st sampling time in May, this was surprisingly not the case for the sun leaves. The results for the May sampling can be explained by the different times of leaf emergence of sun and shade leaves. The shade leaves develop somewhat earlier than the sun leaves in the spring and turn yellow later in the fall (Tanner and Eller 1986). At the time of sampling in May the shade leaves had therefore been exposed to the UV-B radiation for a longer period of time than the sun leaves. Following the full development of the sun leaves the radiation exposure of the shade leaves was reduced with the result that the UV-B absorption over the further course of the growing season was always less for the shade leaves than for the sun leaves. Yang et al. (1995) found that the transmission of UV-B radiation through the leaves of 7 hardwood species was less than 0.1%. The level of transmission of UV-B radiation through a thick forest canopy is therefore likely to be extremely low (McEod and Newsham 1997). This is confirmed in studies by Brown et al. (1994) of the spatial and temporal distribution of UV-B radiation in various forest ecosystems. According to these authors, in forests with a thick canopy less than 1–2% of the incident UV-B radiation reaches the lower levels.

In evaluating pigment concentrations in beech leaves it should be kept in mind that phenylpropanoid synthesis can be stimulated by additional factors including nutrient deficiency, water stress and CO_2 enrichment (Strain and Bazzaz 1983, Bohm 1987, Rufty et al. 1988, Lambers 1993, Lavola and Julkunen-Tiitto 1994, Deckmyn and Impens 1997, Dixon and Paiva 1995, Lovelock et al. 1992, Sullivan and Teramura 1990, Estiarte et al. 1999). Based on studies by Neitzke and Therburg (2000) a possible influence of nutrient deficiency along the study transect on the synthesis of protective pigments can be ruled out, whereas the influence of the temperature of ozone cannot.

Absorption spectra similar to those for the methanolic extracts of the beech leaves, with a broad peak between 270 and 280 nm and a decrease in absorption from 280 to 320 nm, were found by Karabourniotis et al. (1995) for *Olea europaea, Eriobotrya japonica* and *Cydonia oblonga* and by Day et al. (1994) for 14 evergreen and 5 deciduous tree species. A high absorption maximum between 210 and 230 nm is likewise characteristic of absorption spectra for flavonoids (Bornman and Vogelman 1988, Karabourniotis et al. 1995). The location of the absorption maximum at 280 nm is significant in that many organic molecules such as peptides, proteins, lipids and phytochromes also have absorption maxima at 280 nm (Panten et al. 1996). In the present study no attempt was made to determine the chemical nature of the UV-B absorbing compounds in beech leaves, as has been done by Heller et al. (1998). The nature of the phenolic compounds responsible for the observed absorption spectra cannot be inferred from the absorption profiles of known compounds in this case since crude extracts from plant tissues usually contain such varied UV absorbing compounds that any attempt to analyse total absorption profiles would be meaningless (Martin 1970).

In spite of the ability of beech leaves to react to increased UV-B radiation stress with an increased synthesis of UV-B radiation absorbing compounds, beeches appear to be sensitive to UV-B radiation. An impairment of the growth of young beech plants due to currently prevailing UV-B radiation levels was shown in studies by Bogenrieder and Klein (1982) in which an increase in the growth of beech seedlings was observed after UV-B radiation was excluded by means of plexiglass chambers. An impairment of the growth of young beeches due to an increase in UV-B stress was demonstrated by Zeuthen et al. (1997). These authors exposed 5-year-old beech trees in open-top chambers to 2 different UV-B radiation intensities. A simulation of a 14% decrease in stratospheric ozone resulted in a decrease in net photosynthesis, a decrease in chlorophyll fluorescence, a closing of the stomata and an acceleration of senescence by 14 days. Láposi et al. (2002) found that the ambient level of UV-B radiation decreased the maximum photochemical efficiency (F_v/F_m) of dark-adapted leaves, especially at noon. When UV-B radiation was at ambient levels beech leaves contained significantly higher concentrations of UV-B absorbing compounds on the basis of leaf area than when UV-B was excluded. Flavonoid accumulation was found to be more closely correlated with an increase in specific leaf weight than was the case when UV-B radiation was excluded during leaf development.

Day (1993) hypothesizes that the leaves of deciduous trees are more sensitive to an increase in UV-B radiation than are those of evergreen trees. A comparison between deciduous and evergreen trees has shown that there are lower concentrations of UV-B absorbing substances in deciduous trees than in evergreens. Thus, in deciduous trees a greater amount of UV-B radiation reaches the photosynthetically active mesophyll. It is possible that at low elevations and on the slopes of low-lying mountains differences in sensitivity among individual tree species may not play a significant role. Nevertheless, the situation may be different where the beech reaches the limits of its range. However, such speculations must take into account the possibility of the formation of ecotypes or varieties, as demonstrated by BOGENRIEDER and KLEIN (1982) for *Acer pseudoplatanus* and by MCDOUGAL and PARKS (1986) for *Quercus*. The present study indicates that the beech exhibits a fair degree of plasticity in responding to increases in UV-B radiation. From this it can be concluded that beeches should be able to cope with a future increase in UV-B radiation in their environment. However, with regard to such conclusions it must be kept in mind that several stress factors, such as drought, acid rain (PAOLETTI 1998) and ozone (MIKKELSEN and HEIDE-JORGENSEN 1996, ZEUTHEN et al. 1997, RABOTTI and BALLARIN-DENTI 1998) can act simultaneously on forest trees in their natural habitat and that interactions among such factors can intensify or counterbalance their effects.

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