Effects of long-term, elevated ultraviolet-B radiation on phytochemicals in the bark of silver birch (Betula pendula)

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Summary Long-term outdoor experiments were conducted to investigate the effects of elevated ultraviolet-B (UV-B, 280–320 nm) radiation on secondary metabolites (phenolics and terpenoids) and the main soluble sugars (sucrose, raffinose and glucose) in the bark of silver birch (Betula pendula Roth) saplings. Saplings were exposed to a constant 50% increase in erythemal UV irradiance (UV-BCIE; based on the CIE (International Commission on Illumination) erythemal action spectrum) and a small increase in UV-A radiation (320–400 nm) for three growing seasons in an irradiation field in central Finland. Two control groups were used: saplings exposed to ambient radiation and saplings exposed to slightly increased UV-A radiation.

Concentrations of sucrose, raffinose and glucose in bark were higher in UV-treated saplings than in saplings grown in ambient radiation, indicating that stem carbohydrate metabolism was changed by long-term elevated UV radiation. Saplings in the elevated UV-A + UV-B radiation treatment and the UV-A radiation control treatment had significantly increased concentrations of certain UV-absorbing phenolics, such as salidroside, 3,4′-dihydroxypropiophenone-3-glucoside, (+)-catechin and (–)-epicatechin compared with saplings in ambient radiation. In contrast, the radiation treatments had no effect on the non-UV-B-absorbing terpenoids, papyriferic acid and deacetylpapyriferic acid. We conclude that plant parts, in addition to leaves, accumulate specific phenolic UV-filters in response to UV radiation exposure.

Keywords: glucose, phenolics, raffinose, sucrose, terpenoids.

Introduction Potentially damaging ultraviolet-B (UV-B, 280–320 nm) radiation is filtered by flavonoids and phenolic acids in the epidermis of leaves before it can penetrate the inner photosynthetic cells (e.g., Cen and Bornman 1993, Ålenius et al. 1995, Burchard et al. 2000). Certain flavonoids have also been found in the bark of young stems of silver birch (Betula pendula Roth) (Vainiotalo et al. 1991, Julkunen-Tiitto et al. 1996), but it is unknown whether these compounds are involved in protection against the effects of UV-B radiation. Ultraviolet-absorbing phenolics have been found in the walls of cork cells at the bark surface (Taiz and Zeiger 1993) and in resin glands and epithelial hairs (Taipale et al. 1994). The cell cavities of outer cork cells are filled with air (Cutter 1975), and thus do not participate in UV-B-screening. It is possible, however, that phenolic compounds are stored in the living, possibly photosynthetic cells of the phelloderm (secondary cortex) and in secondary phloem (Cutter 1975) below the outer cork cell layers.

Phenolic compounds present in bark have many functions. In addition to their potential role in protection against UV-B radiation stress, they have been shown, in juvenile silver birch, to have a possible role in deterring browsing by mammals (Tahvanainen et al. 1985, 1991 and references therein). For example, platyphyllloside, which is the most abundant phenolic compound in bark of silver birch saplings (Julkunen-Tiitto et al. 1996), has both digestibility and palatability-reducing properties (Sunnerheim et al. 1988). However, the low palatability of silver birch seedlings and saplings to mammal herbivores such as hares is mainly determined by papyriferic acid, which is a triterpenic component present in the resin droplets that are secreted by resin glands onto the outer bark (Tahvanainen et al. 1991, Raatikainen et al. 1992). Unlike the UV-B-absorbing phenolics, terpenoids do not attenuate UV-B radiation, although the resin droplets may cause some reflection or scattering of UV radiation at the stem surface (Vogelmann 1993).

Because of the importance of leaf cells in carbohydrate production, earlier studies focused on effects of UV-B radiation on the concentrations of UV-B-filtering phenolics in leaves, and there has been little research into the effects of UV-B radiation on secondary metabolites in other plant parts. However, it is possible that high doses of UV-B radiation change the concentrations of secondary metabolites in the bark of juvenile trees. The concentrations of antiherbivorous chemicals in
the bark may also change and affect the chemical resistance to mammalian browsers. The purpose of our study, therefore, was to determine whether long-term UV-B exposure affects the concentrations of phenolics and terpenoids in the bark of silver birch saplings.

We also examined whether UV-B radiation affects the concentrations of the main soluble sugars (sucrose, raffinose and glucose) in silver birch stems, because these are involved in the transportation and allocation of assimilated carbon (Avigad and Dey 1997), and UV-B-induced changes in their concentrations may affect tree growth. Changes in sugar concentrations may also affect plant–herbivory interactions, because soluble carbohydrates in stems of juvenile silver birch can stimulate feeding by certain mammalian herbivores (Tahvanainen et al. 1991 and references therein).

Materials and methods

Field experiment
An outdoor UV-B irradiation facility was used for three successive summers (1997–1999). The system consisted of 1.5 × 3.0 m lamp frames, arranged in seven blocks (six in 1997), each containing three frames: an ambient control, an elevated UV-A + UV-B radiation treatment and a UV-A radiation control (ambient UV-B). Six lamps (1.20 m) were mounted on each frame, following “cosine” distribution (Björn 1990), at a height of 0.60 m above the top of the plants. Ambient radiation and shading were provided by unenergized lamps. The elevated UV-A + UV-B radiation treatment was provided by UV-B lamps (UVB-313, Q-Panel, Cleveland, OH) covered with cellulose diacetate filters (0.115 mm, FilmSales, London, U.K.) that transmit UV-B and UV-A radiation but absorb radiation below 290 nm. The lamps were adjusted every minute to elevate erythemal UV irradiance (UV-B CIE; 300–400 nm) by 50%, which corresponds to a 20–25% reduction of the ozone column above central Finland (Björn 1990). The UV-B CIE was based on the CIE (International Commission on Illumination) erythemal action spectrum (McKinley and Diffey 1987). The UV-A radiation control was obtained by covering UV-B lamps with polyester filters (0.125 mm, FilmSales) that absorb UV-B radiation below 313 nm but transmit UV-A radiation. The increase in unweighted UV-A radiation compared with sunlight in the UV-A control treatment was about 0.56–1.12% and in the UV-A + UV-B treatment it was 0.75–1.54%. These increases were calculated from lamp emissions measured (with the same control gear and frames) in a darkened room compared with UV-A radiation measured in sunlight. The emission spectra of the lamps were multiplied by the transmission spectra of the polyester and cellulose diacetate filters, as appropriate, during the course of the experiment. Based on these spectra, we determined the percentage increase in UV-A radiation associated with the increase in UV-B CIE.

A reference UV-B sensor (BW-20 Vital Technologies, Bolton, Ontario, Canada) was located in a UV-A radiation control frame, because the sensor-type has a small residual sensitivity to UV-A radiation. A feedback sensor was placed in an elevated UV-A + UV-B radiation frame. The system used a feedback loop to adjust the lamps. During the experiments, UV-B CIE was continuously monitored using a correction for the drift in the calibration with ambient temperature. The sensors were cross-calibrated to ensure proper functioning of the modulated system, and their output was compared with that of a recently calibrated double monochromator spectroradiometer (Macam SR-9010-PC, Livingston, Scotland). Lamp output was measured indoors in the absence of sunlight with a spectroradiometer. Sunlight spectra were measured outdoors with the spectroradiometer. We continuously monitored photosynthetically active radiation (400–700 nm) with a regularly calibrated quantum sensor (LI-190-SA, Li-Cor, Lincoln, NE) connected to the data logger. The performance of the irradiation system is discussed in more detail in Aphalo et al. (1999).

Silver birch saplings were grown from seeds collected in a silver birch orchard in central Finland. During the first summer, seedlings were grown in 1-l pots filled with soil and fertilized peat (1:1, v/v). The pots were placed beneath the lamp frames in two rows, in an area of 0.80 × 2.40 m, where the UV-B irradiance varied by less than 10%. The seedlings for the seventh block (1998–1999) were grown in the frames of adjacent blocks. The seedlings were fertilized twice with 50 ml of 10% nutrient solution balanced for birch by Ingestad (1962). In the late autumn, the seedlings were planted in soil in the central area under the lamp frames. This area was fertilized with a commercial fertilizer at a rate corresponding to 30 kg N ha–1 in the second spring and to 20 kg N ha–1 in the third spring. The irradiation treatments began on August 13, 1997, May 19, 1998 and May 14, 1999 and ceased in late September of each year. Shoot growth, biomass accumulation and leaf phenolic concentrations of the saplings are reported in Tegelberg et al. (2001).

Chemical analyses
At the end of the third summer, six winter-dormant saplings were taken from each frame. A 10-cm section was cut from the stem of each sapling, 40 cm from the top, and stored in a plastic bag in a freezer (−18 °C). Later, the outer bark and phloem were separated from the xylem with a sharp knife for chemical analyses and dry mass determination. Each sample (200–250 mg) was cut into small pieces and extracted for 2 min in 15 ml of methanol with an Ultra-Turrax T25 homogenizer (Janke and Kunkel, Ika-Labortechnik, Staufen, Germany). The sample was placed on ice for 15 min, extracted again for 2 min and filtered. The residue was incubated on ice for 5 min, extracted for 2 min in 15 ml methanol and filtered. Finally, the residue was incubated on ice for 5 min, extracted in 15 ml of ethanol and filtered. The extracts were combined and the methanol and ethanol evaporated in a rotavapor. The dried sample was dissolved in 10 ml of methanol. Four 1-ml aliquots were dried in a stream of gaseous nitrogen.

Phenolics were analyzed by high performance liquid chromatography (HPLC) according to Julkunen-Tiitto et al. (1996). An HP Series 1100 LC/DAD from Hewlett-Packard
log10-transformed, where necessary, to meet the assumptions and additionally to Tukey's highest significant difference test. The data were submitted to ANOVA for a complete randomized block design of the analysis of variance (ANOVA). The data were standardized with purified tannin from leaves of *Betula nana* (Palo Alto, CA) was used. For the HPLC analyses, the dried samples were dissolved in 1:1 (v/v) water:methanol. Identification of compounds was based on their retention times and UV-spectra monitored at 220, 270, 280, 320 and 360 nm. Quantification was based on commercial standards as follows: salicin (Roth, Karlsruhe, Germany) for salidroside, dehydro-salidroside, (−)-rhododendrin and platylvloside; picein (Extrasyntese, Genay, France) for 3,4-dihydroxypropiophenone-3-glucoside (DHPPG); (−)-catechin (Aldrich, Steinheim, Germany) for (−)-catechin and (−)-epicatechin; chlorogenic acid (Aldrich) for chlorogenic acid and cinnamic acid derivatives; quercetin-3-galactoside (Roth) for quercetin glycoside derivatives and flavonol glycoside; apigenin-7-glucoside (Roth) for apigenin glycoside; and gallic acid (Aldrich) for ellagic acid derivative.

Concentrations of condensed tannins were determined in methanol extracts with a butanol-HCl test (Hagerman 1995), which was standardized with purified tannin from leaves of *Betula nana* L. (dwarf birch).

Terpenoids and sugars were analyzed by capillary gas chromatography (Hewlett-Packard Model 5890 equipped with a HP 5971 Series mass selective detector). Dried samples were dissolved in 300 µl of dimethylformamide and then derivatized with 300 µl of trimethylsilylimidazole in pyridine (7:3, v/v). Each sample was shaken and allowed to react for 20 min. An HP-5MS capillary column (30 m × 0.25 mm I.D.) with a film thickness of 0.25 µm was used. The temperature program was started at 190 °C, and raised to 300 °C at a rate of 8 °C min⁻¹. The interface and injector temperatures were 180 and 250 °C, respectively. The auto-injected volume was 2 µl, and helium was used as a carrier gas. Electron ionization spectra were recorded at 70 eV. Identification of the trimethylsilyl derivatives of the terpenoids and sugars was based on the mass spectra (m/z) using selected ion monitoring (SIM): 147 and 217 for glucose; 73, 217, 361 and 437 for sucrose; 204 and 217 for raffinose; 131, 215, 381 and 472 for papyriferic acid and 131, 215, 382 and 442 for deacetylpapyriferic acid. Commercial standards of sucrose (J.T. Baker, Deventer, Holland), raffinose (Sigma, St. Louis, MO) and glucose (Merck, Darmstadt, Germany) were used to quantify the sugars. Papyriferic acid and deacetylpapyriferic acid were quantified against purified papyriferic acid, which was kindly supplied by Prof. Paul Reichardt, University of Alaska.

**Statistical tests**

The unit of replication used for each variable was the mean of the values measured per frame, i.e., n = 7. The data were log₁₀-transformed, where necessary, to meet the assumptions of the analysis of variance (ANOVA). The data were subjected to ANOVA for a complete randomized block design and additionally to Tukey’s highest significant difference (HSD) multiple comparisons test when the P-value for the F-test for the effect of UV radiation was less than 0.05.

**Results**

Most of the phenolic compounds investigated in silver birch bark were unaffected by elevated UV-A + UV-B radiation, but the concentration of the phenolic acid, DHPPG, was significantly higher in UV-A + UV-B-treated saplings than in ambient controls (Table 1). The concentrations of DHPPG, salidroside (a small-molecular-weight phenolic glucoside), and the main flavonoids in silver birch bark ((+)-catechin and (−)-epicatechin) were higher in UV-A-treated saplings than in ambient controls. The (−)-epicatechin concentration was also significantly higher in saplings in the UV-A treatment than in the UV-A + UV-B treatment (Table 1). Total flavonoid concentration (sum of (−)-catechin, (−)-epicatechin, quercetins, flavonol glycoside and apigenin glycoside) was significantly increased in the UV-A-treated saplings compared with the other saplings (Figure 1). In contrast, the UV radiation treatments had no effect on the main phenolics ((−)-rhododendrin, platylvloside and condensed tannins; Table 1).

The main terpenoids in silver birch bark were identified as papyriferic acid and deacetylpapyriferic acid. The concentrations of these triterpenes were higher than the concentrations of phenolics (Table 1), but there was considerable variation in terpenoid concentrations among individuals. Terpenoids were not significantly affected by the UV treatments.

Raffinose concentration was twofold higher in bark of UV-treated saplings than in bark of control saplings (Figure 2). Raffinose concentration was significantly higher in saplings grown in the UV-A treatment than in saplings grown under control conditions. Compared with the control treatments, elevated UV-A + UV-B radiation significantly increased bark glucose concentrations.

**Discussion**

Phenolics that absorb UV-B radiation commonly accumulate in silver birch leaves in response to elevated UV-B radiation (e.g., Lavola et al. 1997, de la Rosa et al. 2001, Tegelberg et al. 2001). We found that UV exposure also increased the concentrations of several phenolics in bark of silver birch saplings. The increase in the DHPPG concentration in bark in response to elevated UV radiation may be associated with its ability to actively screen UV-B radiation around 300 nm (cf. Lavola et al. 1997). This suggestion is supported by previous findings (Tegelberg et al. 2001) that DHPPG was also increased in UV-B-treated leaves from the same saplings. Although flavonoids such as (+)-catechin and (−)-epicatechin and salidroside increased in response to elevated UV radiation, these compounds cannot screen excess UV radiation efficiently because they absorb the longer wavelengths of UV-B and UV-A radiation only slightly (Hoque and Remus 1999).

Most changes in phenolic concentrations in response to elevated UV radiation were relatively small, indicating that induction of phenolic synthesis by elevated UV radiation was also small. The small effect of enhanced UV radiation on bark phenolic concentrations may be associated with their location in the inner bark, where penetration of UV radiation is reduced.
by the outer cell layers and other chemical and anatomical factors at the stem surface. Similarly, the concentrations of flavonoids and phenolic acids in the inner parts of leaves do not vary greatly in response to elevated UV-B radiation exposure (e.g., Burchard et al. 2000).

The efficiency of UV absorption is affected not only by the concentrations of phenolics, but also by the composition of the phenolic chemofilters. We found that the phenolic composition in bark (Table 1) differed from that in leaves (Tegelberg et al. 2001) from the same saplings. For example, myricetin derivatives, which are the main flavonoids in leaves and which absorb strongly in the longer wavelengths of UV-B and UV-A radiation, were not present in bark cells. Thus, it appears that chemical protection of silver birch against UV stress is less efficient in stems than in photosynthetic plant parts. During the evolution of land plants, UV-B radiation is believed to have been an important factor in the evolution of phenolics (see review by Rozema et al. 1997); however, the evolution of phenolic metabolism in vascular plants has also been affected by other, often biotic, factors. In silver birch bark, the production of UV-B-absorbing phenolics may also have been modified by herbivore pressure, leading to the variable roles of phenolics in defense systems against plant-eating animals.

Biochemical studies have shown that UV-A radiation may regulate the transcription of specific genes involved in biosynthesis of phenolics (e.g., Beggs and Wellmann 1994, Christie and Jenkins 1996, Wilson et al. 1998). Consequently, phenolic concentrations may change as a result of elevated UV-A radiation. The influence of UV-A radiation on phenolic concentrations is not expected to increase much in the future, because the ambient dose of UV-A radiation does not greatly depend on the thickness of the ozone layer (Frederick et al. 1989). On the other hand, we found that changes in phenolic concentrations can be caused by a relatively small increase in UV-A radiation. In silver birch bark, flavonoids, especially (+)-catechin and (–)-epicatechin, were affected more by the small increase (about 1%) in UV-A radiation than by the 50% increase in UV-B radiation (Figure 1, Table 1). Earlier field studies have also shown that concentrations of certain phenolics in leaves of deciduous trees are changed by a small increase in UV-A radiation (Newsham et al. 2001, Tegelberg et al. 2001). Non-UV-B-absorbing terpenoids, which are the main secondary metabolites in silver birch bark, were unaffected by the UV-irradiation treatments. In earlier studies, the production of salicylates, alkaloids and furanocoumarins, which do not strongly participate in UV-B protection, was reduced in leaves subjected to elevated UV-B radiation (Larson et al. 1990, Asthana et al. 1993, Tegelberg and Julkunen-Tiitto 2001). These reductions may have been the result of competition for resources during UV-B stress: if more resources are allocated to chemofilters and cellular damage repair, this may have the effect of reducing synthesis of non-UV-B-screening secondary metabolites. However, despite the high cost of terpenoid

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Table 1. Mean concentrations of secondary chemicals (mg g\(^{-1}\) DW ± SE) in the bark of silver birch saplings grown in the enhanced UV irradiation area for three growing seasons. The result of ANOVA (\(F\)- and \(P\)-values; *** = \(P < 0.001\); ** = \(P < 0.01\); * = \(P < 0.05\)) is presented for the treatment effect. Means with different letters are significantly different (Tukey's HSD, \(P < 0.05\)). Abbreviation: DHPPG = 3,4'-dihydroxypropiophenone-3-glucoside.

<table>
<thead>
<tr>
<th></th>
<th>Ambient radiation</th>
<th>UV-A treatment</th>
<th>UV-A + UV-B treatment</th>
<th>ANOVA</th>
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<td><strong>Phenolics</strong></td>
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<tr>
<td>Salidroside</td>
<td>0.77 ± 0.04 a</td>
<td>1.03 ± 0.06 b</td>
<td>0.91 ± 0.07 ab</td>
<td>6.20 **</td>
</tr>
<tr>
<td>Dehydroxylsalidroside</td>
<td>1.35 ± 0.10</td>
<td>1.83 ± 0.18</td>
<td>1.52 ± 0.15</td>
<td>1.26</td>
</tr>
<tr>
<td>(–)-Rhododendrin</td>
<td>9.60 ± 0.51</td>
<td>10.7 ± 0.81</td>
<td>10.8 ± 0.74</td>
<td>0.93</td>
</tr>
<tr>
<td>Platycylinobioside</td>
<td>25.2 ± 1.25</td>
<td>26.9 ± 1.11</td>
<td>25.9 ± 1.15</td>
<td>0.32</td>
</tr>
<tr>
<td>DHPPG</td>
<td>0.73 ± 0.03 a</td>
<td>0.88 ± 0.04 b</td>
<td>0.89 ± 0.06 b</td>
<td>4.92 *</td>
</tr>
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<td>OH-cinnamic acid deri-</td>
<td>0.27 ± 0.03</td>
<td>0.30 ± 0.04</td>
<td>0.28 ± 0.04</td>
<td>0.03</td>
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<td>vative 1</td>
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<tr>
<td>OH-cinnamic acid deri-</td>
<td>0.52 ± 0.05</td>
<td>0.58 ± 0.06</td>
<td>0.70 ± 0.12</td>
<td>0.99</td>
</tr>
<tr>
<td>vative 2</td>
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<tr>
<td>OH-cinnamic acid deri-</td>
<td>0.11 ± 0.01</td>
<td>0.12 ± 0.01</td>
<td>0.12 ± 0.01</td>
<td>0.19</td>
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<td>Chlorogenic acid</td>
<td>0.22 ± 0.02</td>
<td>0.23 ± 0.04</td>
<td>0.23 ± 0.04</td>
<td>0.01</td>
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<td>(+)-Catechin</td>
<td>5.90 ± 0.35 a</td>
<td>7.69 ± 0.58 b</td>
<td>6.44 ± 0.38 ab</td>
<td>5.47 *</td>
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<tr>
<td>(–)-Epicatechin</td>
<td>2.08 ± 0.17 a</td>
<td>2.78 ± 0.24 b</td>
<td>1.99 ± 0.16 a</td>
<td>6.04 **</td>
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<tr>
<td>Que-3-galactoside</td>
<td>0.58 ± 0.04</td>
<td>0.61 ± 0.07</td>
<td>0.59 ± 0.05</td>
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<tr>
<td>Que-3-glucose + glucuro-</td>
<td>0.21 ± 0.02</td>
<td>0.25 ± 0.03</td>
<td>0.19 ± 0.02</td>
<td>0.64</td>
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<tr>
<td>nide</td>
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<tr>
<td>Que-3-arabinoside</td>
<td>0.19 ± 0.01</td>
<td>0.20 ± 0.02</td>
<td>0.23 ± 0.03</td>
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<td>Flavonol glycoside</td>
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<td>0.14 ± 0.01</td>
<td>0.19 ± 0.02</td>
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<td>Apigenin glycoside</td>
<td>1.07 ± 0.18</td>
<td>1.42 ± 0.20</td>
<td>0.98 ± 0.16</td>
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<td>Ellagic acid derivative</td>
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<td>0.78 ± 0.20</td>
<td>0.45 ± 0.06</td>
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<td>Condensed tannins</td>
<td>25.7 ± 0.87</td>
<td>25.9 ± 0.94</td>
<td>24.3 ± 0.76</td>
<td>0.40</td>
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<td><strong>Terpenoids</strong></td>
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<td>Papyriferic acid</td>
<td>46.5 ± 7.82</td>
<td>46.4 ± 7.70</td>
<td>34.3 ± 4.96</td>
<td>0.64</td>
</tr>
<tr>
<td>Deacetylglpyriferic acid</td>
<td>28.6 ± 5.89</td>
<td>29.1 ± 6.13</td>
<td>29.6 ± 5.80</td>
<td>0.13</td>
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</table>
production (Gershenzon 1994), it was not reduced by our enhanced UV-B radiation treatment and the increases in phenolic concentrations were slight. Thus, in silver birch bark, no clear trade-off was found between the production of UV-B-protective phenolics and non-protective terpenoids. Moreover, there was considerable variation in concentrations of terpenoids among individuals in all of the radiation treatments (Table 1), suggesting that terpenoid production was determined more by the genotype of the individual saplings than by the changing abiotic environmental factor, UV radiation.

The most common phloem translocate is sucrose, but raffinose, which consists of a sucrose and a galactose unit, is also commonly translocated from source to sink (Avigad and Dey 1997). Phloem sap generally does not contain glucose. The soluble sugars, sucrose, raffinose and glucose, accumulated in bark of silver birch saplings during long-term UV radiation exposure, perhaps indicating (1) increased synthesis of photoassimilates in the leaves, (2) disturbed carbon allocation in sinks or (3) the breakdown of storage carbohydrates into soluble sugars (mainly sucrose). Previous UV-B irradiation studies in the field have shown that photosynthetic productivity is unaffected by moderate doses of UV-B radiation; furthermore, possible reductions in leaf biomass, leaf area and carboxylation efficiency in response to elevated UV-B radiation would be expected to lead to reduced productivity (review by Allen et al. 1998, Keiller and Holmes 2001). It appears that the ability to store and metabolize imported sugars in the bark was disturbed by the UV treatment. It is also possible that sucrose and raffinose concentrations were affected by UV-induced changes in the regulatory mechanisms that determine the amount of starch. Moreover, the repair and UV-exclusion processes in UV-treated saplings may have required soluble sugars rather than storage sugars. However, although the growth processes in UV-treated stems were well provided with sugars, Tegelberg et al. (2001) showed that stem diameter growth of the same silver birch saplings was significantly reduced after three growing seasons of exposure to elevated UV-A + UV-B radiation: mean stem diameter of saplings grown in ambient radiation was 12.9 mm, compared with values of 12.8 and 10.9 mm for saplings exposed to the UV-A radiation control and UV-A + UV-B radiation treatments, respectively.
respectively. We suggest, therefore, that metabolic processes that use assimilates for cell growth and formation of cell wall materials slowed in response to elevated UV-B radiation, leading to the accumulation of soluble sugars, particularly glucose. Stem diameter growth, in particular, was reduced during mid- and late summer, when sugars are used for the formation of cell wall materials in the thick walls of late-summer wood cells. Our suggestion is in accordance with that by Gehrke et al. (1995), who reported that the α-cellulose content in leaves decreased when plants were exposed to enhanced UV-B radiation, possibly because of a reduction in cell wall production. However, it is also possible that stem diameter growth in silver birch was affected by other mechanisms sensitive to UV-B radiation, and that decreased sink demand (reduced growth rate) led to the accumulation of soluble sugars in the stems.

In conclusion, the effects of elevated UV radiation on secondary metabolites in bark of silver birch saplings were minor. Certain UV-absorbing phenolic components were increased by the UV-treatments, but terpenoids, which reduce the palatability of plants to mammals, were unaffected. Soluble sugars accumulated in the stems of silver birch saplings in response to elevated UV radiation, possibly because of reduced carbon utilization in sink cells. This accumulation of transportable sugars may affect tree growth and palatability of the trees to certain herbivores.

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