

Phyton (Austria) Special issue: "D. Grill"	Vol. 45	Fasc. 3	(267)-(277)	1.9.2005
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Light and UV Acclimation Responses in Sub-Arctic Evergreens

By

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K e y w o r d s : Mosses, conifer needles, UV-absorbing compounds, waxes.

S u m m a r y

HUTTUNEN S. 2005. Light and UV acclimation responses in sub-arctic evergreens. - *Phyton* (Horn, Austria) 45 (3): (267)-(277).

Late winter and early spring in sub-arctic and arctic ecosystems are characterized by high radiation levels and fluctuations between freezing and thawing temperatures. Evergreens are important key species, and the light and UV doses received by evergreens in the late winter and early spring are high due to reflectance from the long-lasting snow cover on to sites without snow. This paper reviews research on light and UV acclimation in the sub-arctic.

I n t r o d u c t i o n

Most climate models predict the greatest temperature increase due to the future climatic change to occur at the high latitudes (FORTELIUS & al. 1996), and the relative elevation of tropospheric ozone levels will also be remarkable (FOWLER & al. 1999). A new evaluation of responses in the arctic tundra and sub-arctic forest ecosystems is available in the form of an ACIA Scientific Report (Impacts of warming Arctic 2004).

The relative ozone depletion and the relative increase in UV-B radiation are greater at sub-arctic than lower latitudes (MADRONICH & al. 1995), and this may be more important than the absolute radiation levels (BJÖRN & al. 1997). The largest increases in UV levels occur in the springtime, and the warming-related declines in snow and ice cover increase exposure. The total impact is greater than the sum of its parts, such as chemical contaminants, UV, and climatic warming.

In the arctic tundra and sub-arctic ecosystems, the snow cover normally persist into the spring after air temperatures and light have increased to levels suit-

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able for photosynthesis. Bryophytes and lichens (KAPPEN 1993) photosynthesize under snow, but so do also evergreen vascular plants (STARR & OBERBAUER 2003). The probable result is that especially spring conditions with a lengthening snow-free period will affect early active evergreens.

Responses in Plant Structure and Chemistry

Outdoor UV-B supplementation studies with higher plants exposed to radiation from modulated lamp banks have detected some significant responses, but plant responses to UV-B generally seem to be more subtle than expected based on exclusion studies (DAY 2001). The most consistent response in higher plants was an increase in the concentrations of soluble leaf UV-B-absorbing compounds (SEARLES & al. 2001). Phenylpropanoids, e.g. hydroxycinnamic acid, cinnamoyl esters, and flavonoids, including flavones and flavonols, and anthocyanins provide a UV-A and UV-B screen in higher plants (COCKELL & KNOWLAND 1999). The flavonoids responsible for UV screening vary from species to species, and most plants synthesize a range of compounds to provide a more effective screen. So far, most of the studies have been made on summer-green species.

Studies on evergreens have shown that larger quantities of soluble phenolics are produced in warm than in cold years (TURUNEN & al. 1999). UV-B radiation and altitude alter the foliar flavonoid composition of forest tree species, such as Scots and ponderosa pine (LARACINE-PITTET & LEBRETON 1988, WARREN & al. 2002). The responses may be transient or long-lasting. Phenolics increase with needle age in Scots pine (KINNUNEN & al. 1999), black pine (GIERTYCH & al. 1999), and ponderosa pine (WARREN & al. 2002). Enhanced UV-B radiation increased cutinization, wall-bound phenolics as well as flavonoids in Scots pine needles (LAAKSO & al. 2000), which are important protective characteristics during the late winter and early spring.

The natural UV-screening mechanisms in evergreens have been shown to include UV light screening via reflectance of UV light by the epidermis, UV light screening via reduction of transmission by a special anatomical arrangement of epidermal cells and light-reflecting hyaline hypodermal cells, conversion of UV light via fluorescence, and UV light screening by UV-screening substances in cell walls and on surfaces (HOQUE & REMUS 1999). In higher plants, anthocyanins and flavones increase in response to high visible light levels, and UV irradiation induces flavonoids, sinapate esters, isoflavonoids, and psoralens (DIXON & PAIVA 1995), and in evergreens, diacylated flavonol monoglycoside induction, for example, has been detected (JUNGBLUT & al. 1995), and p-coumaric acid, ferulic acid and astragalins have been identified as UV-B-absorbing substances (HOQUE & REMUS 1999).

A growing body of evidence suggests that plants respond to biotic and abiotic stress factors by increasing their capacity to scavenge reactive oxygen species via the phenylpropanoid pathway (GRACE & LOGAN 2000). Further, the production of epicuticular waxes increases (LAAKSO 2001), and changes in wax bio-

synthesis and chemistry (PRUGEL 1994) occur. On the other hand, harsh climatic factors (winter abrasion) and air-borne particles and pollutants erode epicuticular waxes (TURUNEN & HUTTUNEN 1996). Signal transfer from plant surfaces has indicated the role of cuticular waxes in the environmental control of stomatal development (HOLROYD & al. 2002), and environmental factors may further affect the function of plant leaves. Surface structures and epicuticular waxes differ in their composition, water repellency, wettability, and structure due to climatic factors, including the snow cover (RIELEY & al. 1995) and pollution (TURUNEN & HUTTUNEN 1996). The responses of evergreen shrubs to elevated temperatures have also been studied (ARFT & al. 1999), but the studies on enhanced UV and the effects of lengthened spring activity are still few in number.

Anthocyanins have been reported to occur in the mesophyll layers of some evergreen species, e.g. *Mahonia*, *Viburnum* and *Rhododendron* (CHALKER-SCOTT 1999). Prenylpropanoid and flavonoid compounds usually accumulate in the central vacuoles of guard cells and epidermal cells as well as the subepidermal cells of leaves and shoots. Furthermore, some compounds seem to be covalently linked to plant cell walls (HUTZLER & al. 1998). In red mosses, anthocyanins are so firmly wall-bound that they have been recommended for use as cytological stains (GEIGER & al. 1997). The typical red compounds reported from certain *Sphagnum* species, the sphagnorubins A-C, may be chemically related to 3-deoxyanthocyanidins (MUES 2000).

Anthocyanins absorb blue light and reflect red wavelengths, and theoretically, anthocyanins in the upper epidermis or mesophyll of leaves could compete with light harvesting with chlorophyll and carotenoids. NEILL & GOULD 1999 observed that anthocyanin production enhanced the absorbance of green-yellow wavelengths in proportion to the pigment concentration. The reflectance of red light was independent of the leaf anthocyanin content.

Photoinduction of anthocyanin biosynthesis by wavelengths in the UV, visible, and far-red regions, cold temperature, and osmotic induction are the best-known cases of anthocyanin appearance. Other induction factors, e.g. nutrient deficiency and plant hormonal relations, have also been discovered (CHALKER-SCOTT 1999). Anthocyanins are common in some moss species, including Sphagnales, but their importance for the species is not fully understood. Changes in the light climate and hydrology may affect the spectral behaviour of *Sphagnum* canopies and further complicate the interpretation of spectral images (BRYANT & BAIRD 2003).

Waxes and surface-associated flavonoids have not been systematically studied in subarctic and arctic evergreens.

Mosses as Model Plants

Mosses are the simplest land plants and therefore central to the study of plant acclimation, particularly the impacts of UV radiation (COVE & al. 1997). Although some bryophytes constitute a major part of certain vegetation types, knowledge about their responses (GIGNAC 2001) to environmental changes is scant. Some

pioneer and fen and bog mosses occupy open areas, while others prefer shady environments. The common ectohydric mosses have a thin lipid layer and no waxes on their surfaces. Some endohydric species have cuticles and wax deposits on their surfaces, but less protective cell wall structures than higher plants. Some mosses seem to fall between the endo- and ectohydric moss types, as they may or may not have protective cuticles and waxes (PROCTOR 1979, HAAS 1999). This means that mosses have developed their own protective strategies against environmental stress. Numerous secondary metabolites have been found in mosses (ZINSMEISTER & al. 1991). Flavonoids, in particular, perform an important photoprotective function.

MARKHAM 1990 and MUES 2000 demonstrated that flavonoids are the most widespread phenolics in bryophytes. Altogether 356 different flavonoids have been reported (ASAKAWA 1995). Flavonoids from bryophytes contain flavone and flavanol aglycones and glycosides, anthocyanins and derivatives, aurones, biflavonoids, dihydroflavonoids, isoflavones, and triflavones (MUES 2000). The moss phenolic constituents have one, two, or more aromatic rings. The second group contains, among other things, bibenzyls, bisbibenzyls, and flavonoids (MUES & ZINSMEISTER 1988). Studies show that the simpler phenolics occurring in lower plants are equally efficient as the more complex flavonoids in terrestrial higher plants (ROZEMA & al. 2002). The UV response in mosses seems to be different from those seen in higher plants. The few studies made with mosses, e.g. *Polytrichum commune* (BARZIG & al. 1998), *Sphagnum fuscum* (GEHRKE 1998), *Hylocomium splendens*, and *Polytrichum commune* (GEHRKE 1999), indicate no response or a decrease in UV-B-absorbing compounds within a short time frame. A significant decrease in the UV-absorbing compounds of *Polytrichum commune* was observed after the third year (GEHRKE 1999). No short-term response was observed in *Pleurozium schreberi* and *Dicranum scoparium* during a three-month transplantation experiment, but enhanced UV-B slightly increased these compounds in *Hylocomium splendens* in September (TAIPALE & HUTTUNEN 2002). MARKHAM & al. 1998 also found a strong correlation between rising UV-B levels and an increase in the ratio of luteolin to apigenin in *Marchantia polymorpha*.

First, the variability of UV-B-absorbing compounds seems to increase under enhanced UV-B (GEHRKE 1999). TUOMAS & HUTTUNEN 2003 observed first, after two months of enhanced UV-B, a statistically significant increase in UV-B-absorbing pigments in *Pleurozium schreberi*. Later on, after two summers of enhanced UV-A and UV-B differential inhibitory responses were observed (LAPPALAINEN & al. 2005). In *Pleurozium schreberi*, screening compounds, flavone apigenin and two trisaccharide flavones, have been found (VANDERKERHOVE 1980, MARKHAM 1988, ZAPP 1992). An inhibitory response was also found in *Polytrichum juniperinum* (TUOMAS & HUTTUNEN 2003). The differences seem to be related to the fact that, of the many flavonoids, only a few are UV-responsive. It seems evident that, in *Pleurozium schreberi*, the relationship between luteolin and apigenin is important.

Past Responses

In the 1990's, a stratospheric ozone loss was documented over the northern hemisphere. The most severe depletion was usually measured during the early spring (JOKELA & al. 1995, TAALAS & al. 1995a), but a slight upward trend in UV throughout the year has been documented in northern Europe (KAUROLA & al. 2000). Ozone depletion in the stratosphere has already affected the penetration of solar radiation at the UV-B wavelengths 280 - 315 nm. The scenario involves an up to 60 % springtime increase in UV radiation at subarctic latitudes (TAALAS & al. 1995b). The increasing atmospheric carbon dioxide concentrations are expected to cause cooling of the lower stratosphere. This could enhance the formation of polar clouds, which convert ozone-depleting species into active forms (AUSTIN & al. 1992). However, pyranometric measurements of global radiation and remote sensing techniques of UV data are rare in northern areas, and reconstruction methods may thus be needed (BODEKER & MCKENZIE 1996, BORDEWIJK & al. 1995).

MARKHAM & al. 1990 proposed a novel method for the determination of historical ozone level trends in the Antarctica, which involved quantitative analysis of flavonoids in herbarium specimens of the moss *Bryum argenteum*. We applied this idea to subarctic herbarium moss species. We studied whether moss species reflect changes in the global radiation climate through their methanol-extractable compound concentrations, whether this relation can be used as an indicator of the past radiation climate, and which species seem to indicate the changes in radiation climate (HUTTUNEN & al. 2005a,b). The results encourage further studies both with environmental specimen bank samples and with herbarium specimens. But they also point out latitudinal and altitudinal differences.

Moss Acclimation and Cuticular Waxes

We need more detailed information about the chemistry of extant bryophyte cuticles. Moss cuticular and wax chemistry is poorly known (PROCTOR 1979, HAAS 1982, 1999). Sporophyte and gametophyte waxes and UV-screening compounds differ (HUTTUNEN & VIRTANEN 2005). Scientists have pointed out that protonemata are non-wettable (DUCKETT & al. 1998), a phenomenon often enhanced by surface waxes. This is certainly related to the prevention of waterlogging in situations where this would significantly depress photosynthesis, e.g. in the leaves of mosses in rock crevices and on banks. The waxes of *Polytrichum commune* (PROCTOR 1979), *Polytrichum longisetum*, *P. ohioense*, *P. formosum*, *P. sexangulare*, and *P. commune* (CLAYTON-GREENE & al. 1985), the sporophyte capsules of *Polytrichastrum alpinum*, *Polytrichum commune*, *P. formosum*, *P. Juniperinum* (incl. gametophytes), *P. piliferum*, *P. Subpilosum*, and *P. strictum* (NEINHUIS & JETTER 1995), and chemistry have been studied by HAAS & al. 1978. However, no research on the acclimation and adaptation of wax or screening compounds in polar areas was found (HUTTUNEN & VIRTANEN 2005).

Herbarium moss specimens reflected changes in UV-B-absorbing compounds and the morphology and structure (specific surface area, waxes) of gametophytes, which correspond to the changes of surface global radiation or UV-B at the site (HUTTUNEN & al. 2005ab). The polar mountain hair moss *Polytrichastrum alpinum* (COLLINS 1976, HUTTUNEN & VIRTANEN 2005) is an arctic alpine species found over large areas, and a key species of special interest in view of enhanced temperature and UV-B responses. New phylogenetic analyses of Polytrichales lend support to the recognition of Polytrichales as a monophyletic entity (HYVÖNEN & al. 2004). Among mosses, the leaves of Polytrichaceae are the closest functional parallels to the leaves of vascular plants.

Moss species with special protective features, such as hairs, waxes, and cuticles, and the phylogeny of their protective functions need to be studied further. Wax functional aspects (WAGNER & al. 2003) are known in higher plants, but mosses have not been studied under fluctuating climatic conditions (for water repellence/wettability). Much attention has been paid to the phenolics associated with the surface of higher plants, i.e. leaf waxes and bud exudates, and the type of compound found is usually different from that occurring within the plant. In the case of flavonoids, the surface compounds are highly methylated and lack sugar substitution (HARBORNE 1989). There is a need to differentiate surface substances and use a combination of microscopy and chemistry to detect functional responses and to evaluate their importance.

Experimental Research

The first in situ enhanced UV-B experiment with Scots pine was established in 1996, to study the long-term effects of UV enhancement on evergreens during the whole four-year life cycle of Scots pine needles (LAAKSO & al. 2000, KINNUNEN & al. 2001, LAAKSO & al. 2001, LATOLA & al. 2001). The research on UV-B acclimation in evergreens - with particular reference to mosses as model plants (2001 - 2003) - has concentrated on three different aspects: 1) enhanced UV-A, UV-B, and PAR response of key moss species in situ (HUTTUNEN & al. 2005a,b, LAPPALAINEN & al. 2005) and in transplantations with and without enhanced UV-B (TAIPALE & HUTTUNEN 2002), 2) functional and structural responses of different (e.g. rock and bank) moss species in situ (e.g. sand dunes) at wind-exposed or snowbed sites at Pallas and other mountains, and 3) past responses of UV-B-absorbing compounds in herbarium and environmental specimen bank specimens (HUTTUNEN & al. 2005a,b).

Surface Responses in a Changing Climate

Deposited particles on evergreen surfaces enhance water loss through the polluted surface due to their hygroscopic action. Thin water films decrease cuticu-

lar resistance, leading to gas deposition on the plant surface (BURKHARDT & EIDEN 1994).

Probably the most stressful time for sub-arctic plants is the spring, when the solar radiation dose with UV received by conifers and evergreens emerging under from the snow cover may be particularly high. As cuticular waxes seem to play a role in the environmental control of stomatal development (HOLROYD & al. 2002), the observations on malformation, delayed biosynthesis of epicuticular waxes, and deformed stomatal complexes after acid rain and exposure to gaseous pollutants or metal treatments (TURUNEN & HUTTUNEN 1991, PRUGEL 1994, TURUNEN & al. 1995, HUTTUNEN & MANNINEN 2005) have functional importance, especially in leaves with a long life-span. KOPPEL & HEINSOO 1994 found that the cuticular resistance of *Picea abies* needles declined gradually along with needle age. In four-year-old needles it constituted about half of that in current-year needles.

In Finnish Lapland, the geographical patterns of wax erosion rate, annual needle wettability change, and sulphur accumulation in 1-year-old wintered needles coincided on a regional scale, with a wax erosion rate of > 35% and an annual needle wettability change of > 6 degrees. Surface wettability increased in the north, but the northernmost surfaces exhibited a major annual needle wettability change and wax erosion rate (TURUNEN & HUTTUNEN 1996).

There are two ways in which epicuticular waxes may facilitate plant survival at sub-zero temperatures. One way is by reducing winter desiccation in evergreen species. The other is that leaves with surface moisture freeze at higher temperatures than comparable leaves with dry exterior surface (JENKS & ASHWORTH 1999). A strict chemical criterion of wax is the presence of an ester of a long-chain acid and a long-chain alcohol (HAMILTON 1995). However, too little is known about the relative absorbance of waxes and related surface screening compounds to speculate on the relative importance of waxes in light and UV acclimation. Further studies on molecular biology and the biodiversity of epicuticular waxes in sub-arctic plants will enhance our understanding of the future evergreen responses to the changing climate.

References

- ARFT A.M., WALKER M.D. & al. 1999. Response patterns of tundra plant species to experimental warming: meta-analysis of the International Tundra Experiment. - *Ecological Monographs* 69: 491-511.
- ASAKAWA Y. 1995. Chemical constituents of the bryophytes. - *Progress in the Chemistry of Organic Natural Products* 65: 618pp.
- AUSTIN J. BUTCHART N. & SHINE P. 1992. Possibility of an Arctic ozone hole in a doubled-CO₂ climate. - *Nature* 360: 221-225.
- BARZIG M., SCHNEIDER K. & GEHRKE C. 1998. Effects of UV-b radiation on fine structure, carbohydrates, and pigments in *Polytrichum commune*. - *Bryologist* 101(3): 357-365.
- BJÖRN L.O., CALLAGHAN T., GEHRKE C., GUNNARSSON T., HOLMGREN B., JOHANSSON U., SNOGERUP S., SONESSON M., STERNER O. & YU S-G. 1997. Effects on subarctic vegetation of enhanced UV-B radiation. - In: LUMSDEN P.L. (Ed.), *Plants and UV-B: responses to environmental change*, pp. 233-246. - Cambridge University Press.

- BODEKER G. E. & MCKENZIE R.L. 1996. An algorithm for inferring surface UV irradiance including cloud effects. - *Journal of Applied Meteorology* 35: 1860-1877.
- BORDEWIJK J.A., SLAPER H., REINEN A. J. M. & SCHLAMANN E. 1995. Total solar radiation and the influence of clouds and aerosols on the biologically effective UV. - *Geophysical Research Letters* 22: 2151-2154.
- BRYANT R.G. & BAIRD A.J. 2003. The spectral behaviour of *Sphagnum* canopies under varying hydrological conditions. - *Geophysical Research Letters* 30(3): 1-4.
- BURKHARDT J. & EIDEN R. 1994. Thin water films on coniferous needles. - *Atmospheric Environment* 28(12): 2001-2017.
- CHALKER-SCOTT L. 1999. Environmental significance of anthocyanins in plant stress responses. Invited Review. - *Photochemistry and Photobiology* 70(1): 1-9.
- CLAYTON-GREENE K.A., COLLINS N.J., GREEN T.G.A. & PROCTOR M.C.F. 1985. Surface wax, structure and function in leaves of *Polytrichaceae*. - *J. Bryol.* 13: 549-562.
- COCKELL C. & KNOWLAND J. 1999. Ultraviolet radiation screening compounds. - *Biol.Rev.* 74: 311-345.
- COLLINS N.J. 1976. Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. - *Oikos* 27: 389-401.
- COVE D., KNIGHT C.D. & LAMBARTER T. 1997. Mosses as model systems. - *Trends in Plant Science* 2: 99-105.
- DAY T.A. 2001. Ultraviolet radiation and plant ecosystems. - In: COCKELL C.S. & BLAUSTEIN A.R. (Eds.), *Ecosystems, evolution and ultraviolet radiation*, pp. 80-117. - Springer Verlag.
- DIXON R. A. & PAIVA N. L. 1995. Stress-induced phenylpropanoid metabolism. - *The Plant Cell* 7: 1085-1097.
- DUCKETT J.G., SCHMID A.M. & LIGRONE R. 1998. Protonemal morphogenesis. - In: BATES J.W., ASHTON N.W. & DUCKETT J.G. (Eds.), *Bryology for the twenty-first century*, pp. 223-246. - British Bryological Society.
- GEHRKE C. 1998. Effects of enhanced UV-B radiation on production-related properties of a *Sphagnum fuscum* dominated subarctic bog. - *Functional Ecology* 12: 940-947.
- 1999. Impacts of enhanced ultraviolet-B radiation on mosses in a subarctic heath ecosystem. - *Ecology* 80: 1844-1851.
- GEIGER H., SEEGER T., ZINSMEISTER H.D. & FRAHM J-P. 1997. The occurrence of flavonoids in arthrodontous mosses - an account of the present knowledge. - *J. Hattori Bot. Lab.* 83: 273-308.
- GIGNAC D.L. 2001. Bryophytes as indicators of climate change. - *The Bryologist* 104: 410-420.
- GIERTYCH M.J., KAROLEWSKI P. & DE TEMMERMAN L.O. 1999. Foliage age and pollution alter content of phenolic compounds and chemical elements in *Pinus nigra* needles. - *Water, Air and Soil Pollution* 110: 363-377.
- GRACE S.G. & LOGAN B.A. 2000. Energy dissipation and radical scavenging by the plant phenylpropanoid pathway. - *Phil. Trans. R. Soc. Lond. B* 355: 1499-1510.
- FORTELIUS C., HOLOPAINEN E., KAUROLA J., RUOSTEENOJA K. & RÄISÄNEN J. 1996. Climate models and scenarios. - In: ROOS J. (Ed.), *The finnish research programme on climate change*. - Publications of the Academy of Finland 4: 43-49.
- FOWLER D., CAPE N.J., COYLE M., FLECHARD C., KUYLENSTIERNA J., HICKS K., DERWENT D., JOHNSON C. & STEVENSON D. 1999. The global exposure of forests to air pollutants. - *Water, Air and Soil Pollution* 116: 5-32.
- HAAS K. 1982. Surface wax of *Andreaea* and *Pogonatum* species. - *Phytochemistry* 21(3): 657-659.
- 1999. Phytochemische und rasterelektronenmikroskopische Untersuchungen zum Oberflächenwachs von Laubmoosen (*Bryatae*), pp. 93. - Verlag Grauer, Stuttgart.
- , BUCHLOCH G., BAYDUR B. & TERTINEGG W. 1978. Alkane patterns in *Polytrichum* and *Porella* species. - *Z. Pflanzenphysiol* Bd. 86: 389-394.
- HAMILTON R.J. 1995. Analysis of waxes. - In: HAMILTON R. (Ed.), *Waxes. Chemistry, molecular biology and functions*, pp. 311-342. - The Oily Press, Dundee.
- HARBORNE J.B. 1989. General procedures and measurement of total phenolics. - *Methods in plant biochemistry* 1: 1-28.

- HOLROYD G.H., HETHERINGTON A.M. & GRAY J.E. 2002. A role for the cuticular waxes in the environmental control of stomatal development. - *New Phytologist* 153: 433-439.
- HOGUE E. & REMUS G. 1999. Natural UV-screening mechanisms of Norway spruce (*Picea abies* L.) needles. - *Photochemistry and Photobiology* 69(2): 177-192.
- HUTTUNEN S. & MANNINEN S. 2005. Scots pine and the changing environment- needle responses. - *Polish Botanical Studies* (in press).
- & VIRTANEN V. 2005. Wax and UV-B -absorbing compounds of *Polytrichastrum alpinum* from different climatic regions. - In: KINNUNEN H. & HUTTUNEN, S. (Eds.), *Proceedings of the meeting forests under changing climate, enhanced UV and air pollution*, pp. 17-21; August 25-30, 2004. Oulu, Finland, Department of Biology, Thule Institute, University of Oulu. - Oulu University Press.
- , LAPPALAINEN N.M. & TURUNEN J. 2005a. UV -absorbing compounds in subarctic herbarium bryophytes. - *Environmental Pollution* 133: 303-314.
- , — , JAAKOLA N., KOSONEN M. & TUSA P. 2004. Evergreen plants and increasing UV in the subarctic. - In: STRAND K., TASKINEN P. & KALLIO K. (Eds.), *Proceedings of the Thule science day. - Northern Dimension and Arctic Environments*, November 25, 2003: 27-30.
- , TAIPALE T., LAPPALAINEN N.M., KUBIN E., LAKKALA K. & KAUROLA J. 2005b. Environmental specimen bank samples of *Pleurozium schreberi* and *Hylocomium splendens* as indicators of the radiation environment at the surface. - *Environmental Pollution* 133: 315-326.
- HUTZLER P., FISCHBACH R., HELLER W., JUNGBLUT T.P., RAUBER S., SCHMITZ R., VEIT M., WEISSENBOCK G. & SCHNITZLER J.-P. 1998. Tissue localization of phenolic compounds in plants by confocal laser scanning microscopy. - *Journal of Experimental Botany* 49(323): 953-965.
- HYVÖNEN J., KOSKINEN S., SMITH MERRILL G.L., HEDDER T.A. & STENROOS S. 2004. Phylogeny of the Polytrichales (*Bryophyta*) based on simultaneous analysis of molecular and morphological data. - *Molecular Phylogenetics and Evolution* 31: 915-928.
- IMPACTS OF A WARMING ARCTIC. ARCTIC CLIMATE IMPACT ASSESSMENT. 2004. - Cambridge University Press. 139 pp.
- JENKS M.A. & ASHWORTH E.N. 1999. Plant epicuticular waxes: function, production and genetics. - *Horticultural Reviews* 23: 2-68.
- JOKELA K., LESZCZYNSKI K., VISURI R. & YLIANTTILA L. 1995. Increased UV exposure in Finland in 1993. - *Photochemistry and Photobiology* 62: 101-107.
- JUNGBLUT T.P., SCHNITZLER J.-P., HELLER W., HERTKORN N., METZGER J.W., SZYMCAK W. & SANDERMANN H. 1995. Structures of UV-B induced sunscreen pigments of the Scots pine (*Pinus sylvestris* L.). - *Angew. Chem. Int. Ed. Engl.* 34: 312-314.
- KAPPEN L. 1993. Plant activity under snow and ice, with particular reference to lichens. - *Arctic* 46(4): 297-302.
- KAUROLA J., TAALAS P. & KOSKELA T. 2000. Long-term variations of UV-B doses at three stations in northern Europe. - *Journal of Geophysical. Research* 105: 813-820.
- KINNUNEN H., LAAKSO K. & HUTTUNEN S. 1999. Methanol-extractable UV-B absorbing compounds in Scots pine needles. - *Chemosphere, Global Change Science* 1: 455-460.
- , HUTTUNEN S. & LAAKSO K. 2001. UV-absorbing compounds and waxes of Scots pine needles during a third growing season of supplemental UV-B in the field. - *Environmental Pollution* 112(2): 215-220.
- KOPPEL A. & HEINSOO K. 1994. Variability in cuticular resistance of *Picea abies* (L.) Karst. and its significance in winter desiccation. - *Proc. Estonian Acad. Scie. Ecol.* 4 (2): 56-63.
- LAAKSO K. 2001. Leaf and needle characteristics of two climax tree species, Holm oak (*Quercus ilex* L.) and Scots pine (*Pinus sylvestris* L.), in elevated-ozone environments in Italy and Finland. - Master's Thesis. Department of Biology, University of Oulu, 46pp.
- , SULLIVAN J.H. & HUTTUNEN S. 2000. The effects of UV-B radiation on epidermal anatomy in loblolly pine (*Pinus taeda* L.) and Scots pine (*Pinus sylvestris* L.). - *Plant, Cell and Environment* 23: 461-472.

- , KINNUNEN H. & HUTTUNEN S. 2001. The glutathione status of mature Scots pines during the third season of UV-B radiation exposure. - *Environmental Pollution* 111(2): 349-354.
- LATOLA K., KINNUNEN H. & HUTTUNEN S. 2001. Needle ontogeny of mature Scots pines under enhanced UV-B radiation. - *Trees* 15 (6): 346-352.
- LAPPALAINEN N., HUTTUNEN S. & PERÄLÄ H. 2005. Acclimation of a moss *Pleurozium schreberi* (Britt.) Mitt. in situ to ultraviolet radiation. - In: KINNUNEN H. & HUTTUNEN S. (Eds.), *Proceedings of the meeting forests under changing climate, enhanced UV and air pollution*, pp. 46-51, August 25-30, 2004. Oulu, Finland, Department of Biology, Thule Institute, University of Oulu. - Oulu University Press.
- LARACINE- PITTET C. & LEBRETON P. 1988. Flavonoid variability within *Pinus sylvestris*. - *Phytochemistry* 27: 2663-2666.
- MADRONICH S., MCKENZIE R., CALDWELL M.M. & BJÖRN L.O. 1995. Changes in ultraviolet radiation reaching the earth's surface. - *Ambio* 24: 143-52.
- MARKHAM K.R. 1988. Distribution of flavonoids in the lower plants and its evolutionary significance. - In: HARBORNE J.B. (Ed.), *The flavonoids*, pp. 427-486. - London, Chapman and Hall Ltd.
- 1990. Bryophyte flavonoids, their structures, distribution, and evolutionary significance. - In: ZINSMEISTER H.D. & MUES R. (Eds.), *Bryophytes. Their chemistry & chemical taxonomy*, pp. 143-159. - Oxford Science Publications.
- , RYAN K.G., BLOOR S.J. & MITCHELL K.A. 1998. An increase in the luteolin: apigenin ratio in *Marchantia polymorpha* on UV-B enhancement. - *Phytochemistry* 48: 791-794.
- , FRANKE A., GIVEN D.R. & BROWNSEY P. 1990. Historical antarctic ozone level trends from herbarium specimen flavonoids. - *Bulletin de Liaison-Groupe Polyphenols* 15: 230-235.
- MUES R. 2000. Chemical constituents and biochemistry. - In: SHAW A.J. & GOFFINET B. (Eds.), *Bryophyte biology*, pp. 150-181. - Cambridge University press.
- & ZINSMEISTER, H.D. 1988. The chemotaxonomy of phenolic compounds in bryophytes. - *Journal of Hattori Botanical Laboratory* 64: 109-141.
- NEILL S. & GOULD K.S. 1999. Optical properties of leaves in relation to anthocyanin concentration and distribution. - *Can.J.Bot.* 77: 1777-1782.
- NEINHUIS J. & JETTER R. 1995. Ultrastructure and chemistry of epicuticular wax crystals in polytrichales sporophytes. - *Journal of Bryology* 18: 399-406.
- PRUGEL B. 1994. Contribution à l'étude des modifications chimiques des cires cuticulaires de *Picea abies* (L.) karst. et de *Picea sitchensis* (Bong.) Carr. en relation avec le déperissement forestier et l'augmentation du CO₂ dans l'atmosphère. - *Dissertation Université de Nancy I* 73 pp.
- PROCTOR M. F. F. 1979. Surface wax on the leaves of some mosses. - *Journal of Bryology* 10: 531-538.
- RASHOTTE A.M. & FELDMANN K.A. 1998. Correlations between epicuticular wax structures and chemical composition in *Arabidopsis thaliana*. - *Int. J. Plant. Sci.* 159: 773-779.
- RIELEY G., WELKER J.M., CALLAGHAN T.V. & ELINGTON G. 1995. Epicuticular waxes of two arctic species: compositional differences in relation to winter snow cover. - *Phytochemistry* 38: 45-52.
- ROZEMA J., BJÖRN L.O., BORMANN J.F., GABERSCIK A., HÄDER D-P., TROST T., GERM M., KLISCH M., GRÖNIGER A., SINHA R.P., LEBERT M., HE Y-Y., BUFFONI-HALL R., DE BAKKER N.V.J., VAN DE STAAL J. & MEIJKAMP B.B. 2002. The role of UV-B radiation in aquatic and terrestrial ecosystems - an experimental and functional analysis of the evolution of UV-B absorbing compounds. - *Journal of Photochemistry and Photobiology B. Biology* 66: 2-12.
- SEARLES P.S., FLINT S.D. & CALDWELL M.M. 2001. A meta-analysis of plant field studies simulating stratospheric ozone depletion. - *Oecologia* 127: 1-10.
- STARR G. & OBERBAUER S.F. 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. - *Ecology* 84 (6): 1415-1420.

- TAALAS P., DAMSKI J., KORPELA A., KOSKELA T. & KYRÖ E. 1995a. - In: WANG W.-C. & ISAKSEN I.S.A. (Eds.), Atmospheric ozone as a climate gas, pp. 411-426. - NATO ASI Series, Vol. I 32, Springer Berlin.
- , KOSKELA T. KYRÖ E., DAMSKI J. & SUPPERI A. 1995b. Ultraviolet radiation in Finland, pp.83-91. - In: ROOS J. (Ed.), The Finnish research programme on climate change, final report. - The Academy of Finland.
- TAIPALE T. & HUTTUNEN S. 2002. Moss flavonoids and their ultrastructural localization under enhanced UV-B radiation. - Polar Research 38: 211-218.
- TUOMAS N. & HUTTUNEN S. 2003. Acclimation of a moss *Polytrichum juniperinum* Hedw. to light and ultraviolet radiation. - In: HONKANEN J.O. & KOPONEN P.S. (Eds.), Sixth Finnish conference of environmental sciences current perspectives in environmental science and technology, pp. 266-269. - University of Joensuu, Joensuu.
- TURUNEN M. & HUTTUNEN S. 1991. Effects of simulated acid rain on the epicuticular wax of Scots pine needles under northerly conditions. - Can. J. Bot. 69: 412-419.
- & — 1996. Scots pine needle surfaces on radial transects across the north boreal area of Finnish Lapland and the Kola Peninsula of Russia. - Environmental Pollution 93(2): 175-194.
- , —, BÄCK J. & LAMPPU J. 1995. Acid rain-induced changes in cuticles and Ca distribution of Scots pine and Norway spruce seedlings. - Can. J. For. Res. 25: 1313-1325.
- , HELLER W., STICH S., SANDERMANN H., SUTINEN M.-L. & NOROKORPI Y. 1999. The effects of UV exclusion on the soluble phenolics of young Scots pine seedlings in the subarctic. - Environmental Pollution 106: 219-228.
- VANDERKERKHOVE O. 1980. Über die Verbreitung von Flavonoiden bei pleurokarpen Laubmoosen. II. Apigenin und Apigenin-7-rhamnoglucosid bei *Pleurozium schreberi* (Willd.) - Mitt. Z. Pflanzenphysiol. Bd. 100: 369-372.
- ZAPP J. 1992. Phytochemische Untersuchungen an ausgewählten Lebermoosen der Gattung *Anastomophyllum* sowie der beiden laubmoose *Dicranum scoparium* und *Pleurozium schreberi*. - Thesis Univ. d. Saarlandes, p. 127.
- ZIINSMEISTER H. D., BECKERT H. & EICHER T. 1991. Bryophytes, a source of biologically active, naturally occurring material? - Angew. Chemistry. Int. Ed. Engl. 30: 130-147.
- WAGNER P., FURSTNER R., BARTHOLOTT W. & NEINHUIS C. 2003. Quantitative assessment to the structural basis of water repellency in natural and technical surfaces. - Journal of Experimental Botany 54 (385): 1295-1303.
- WARREN J.M., BASSMANN J.H., MATTINSON D.S., FELLMANN J.K., EDWARDS G.E. & ROBBERECHT R. 2002. Alteration of foliar flavonoid chemistry induced by enhanced UV-B radiation in field-grown *Pinus ponderosa*, *Quercus robur* and *Pseudotsuga menziesii*. - Journal of Photochemistry and Photobiology B: Biology 66: 125-133.

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Jahr/Year: 2005

Band/Volume: [45_3](#)

Autor(en)/Author(s): Huttunen S.

Artikel/Article: [Light and UV Acclimation Responses in Sub-Arctic Evergreens. 267-277](#)