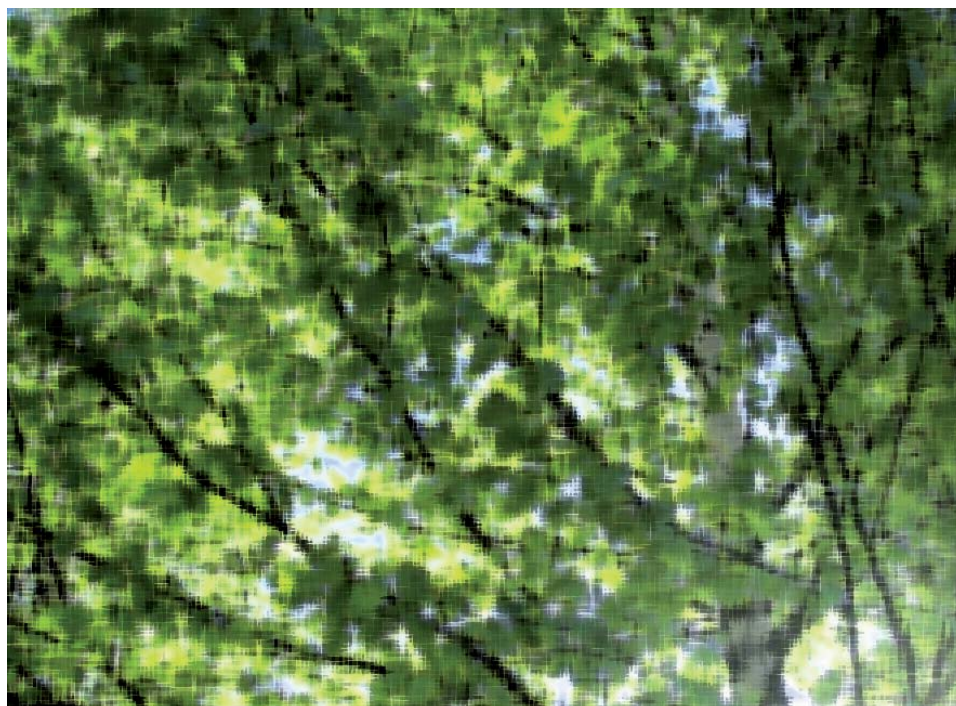


Titta Kotilainen

Solar UV Radiation and Plant Responses

Assessing the Methodological Problems in
Research Concerning Stratospheric
Ozone Depletion



Titta Kotilainen

Solar UV Radiation and Plant Responses

Assessing the Methodological Problems in Research Concerning Stratospheric Ozone Depletion

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303 toukokuun 7. päivänä 2010 kello 12.

Academic dissertation to be publicly discussed, by permission of the Faculty of Mathematics and Science of the University of Jyväskylä, in building Ambiotica, hall YAA303, on May 7, 2010 at 12 o'clock noon.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2010

Solar UV Radiation and Plant Responses

Assessing the Methodological Problems in
Research Concerning Stratospheric Ozone Depletion

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 207

Titta Kotilainen

Solar UV Radiation and Plant Responses

Assessing the Methodological Problems in
Research Concerning Stratospheric Ozone Depletion



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2010

Editor

Anssi Lensu

Department of Biological and Environmental Science, University of Jyväskylä

Pekka Olsbo

Publishing Unit, University Library of Jyväskylä

Jyväskylä Studies in Biological and Environmental Science

Editorial Board

Jari Haimi, Anssi Lensu, Timo Marjomäki, Varpu Marjomäki

Department of Biological and Environmental Science, University of Jyväskylä

Cover picture by Titta Kotilainen

URN:ISBN:9789513939069

ISBN 978-951-39-3906-9 (PDF)

ISBN 978-951-39-3819-2 (nid.)

ISSN 1456-9701

Copyright © 2010, by University of Jyväskylä

Jyväskylä University Printing House, Jyväskylä 2010

ABSTRACT

Kotilainen, Titta

Solar UV radiation and plant responses: Assessing the methodological problems in research concerning stratospheric ozone depletion

Jyväskylä: University of Jyväskylä, 2010, 45 p.

(Jyväskylä Studies in Biological and Environmental Science,

ISSN 1456-9701; 207)

ISBN 978-951-39-3906-9 (PDF), 978-951-39-3819-2 (nid.)

Yhteenvedo: Auringon UV-säteily ja kasvien vasteet: otsonikatoon liittyvien tutkimusten menetelmien arviointia

Diss.

My objective in this thesis was to evaluate the effect of both UV-B and UV-A radiation on different plant responses and, via plants, on decomposition. To achieve this, I compared the responses of three tree species in the family Betulaceae to solar UV-B and UV-A radiation in field and outdoor experiments, using plastic films excluding part of the radiation. Laboratory experiments were conducted to assess the effects of litter grown under different UV treatments on soil fauna and soil respiration and to measure the decomposition rate. The results showed that individual phenolic metabolites were variably affected by the UV treatments and in some cases the UV effect varied even during the growing season. Further changes were measured in the carbon content and cell wall chemistry of plant litter. Changes in the litter chemistry were transferred to soil respiration. As a whole, the results of this thesis emphasize the role of UV radiation as an informational signal spurring photomorphogenetic effects in terrestrial plants and show that those effects can be transferred to decomposition processes as well. My concomitant objective was to develop new methods and models for assessing the validity of previous experiments mimicking the increased levels of UV-B radiation due to stratospheric ozone depletion. To achieve this, published action spectra used as biological spectral weighting functions (BSWFs) were compared to measured plant responses in order to estimate the enhancement errors in past experiments with supplemental UV-B radiation. Based on my assessment, it is possible that in part of the previous experiments the under- or overestimation of the effect of ozone depletion is large enough to distort some conclusions. Findings in this thesis emphasize the importance of appropriate methodology, regarding sampling, measuring methods, and choosing a BSWF closely representing the measured response.

Keywords: Action spectra; Betulaceae; litter decomposition; plant phenolics; soil respiration; UV radiation

Titta Kotilainen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Titta Kotilainen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
titta.kotilainen@jyu.fi

Supervisors Docent Pedro J. Aphalo
Department of Biosciences
P.O. Box 65
FI-00014 University of Helsinki
Finland

Docent Jari Haimi
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Professor Jarmo Holopainen
Department of Environmental Science
University of Eastern Finland
P.O. Box 1627
FI-70211 Kuopio
Finland

Dr. M. Cecilia Rousseaux
CRILAR-CONICET
Entre Rios y Mendoza s/n
5301 Anillaco, La Rioja
Argentina

Opponent Dr. Nigel D. Paul
Department of Biological Sciences, I.E.N.S.
Lancaster University
LA1 4YQ, Lancaster
U.K.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

1	INTRODUCTION	7
1.1	Stratospheric ozone depletion, climate change and UV-B radiation.....	7
1.2	UV radiation and plant responses.....	8
1.3	Effects of UV radiation on terrestrial ecosystems	10
1.4	Tackling the problem of varying spectra from the sun compared to UV lamps.....	11
2	OBJECTIVES	13
3	MATERIALS AND METHODS.....	15
3.1	Field experiments (I and III)	15
3.1.1	General design of the field experiments	15
3.1.2	Field experiment year 2004 (I).....	16
3.1.3	Field experiment year 2005 (III).....	16
3.2	Decomposition experiments (II).....	17
3.2.1	General design of the decomposition experiments.....	17
3.2.2	Microcosms with soil and litter.....	17
3.2.3	Microcosms with woodlice and litter	17
3.3	Outdoor experiment (IV)	17
3.4	Modelling experiment (V).....	18
3.5	Analyses	19
3.5.1	Chemical analyses and plant growth measurements	19
3.5.2	Data analyses.....	20
4	RESULTS AND DISCUSSION.....	22
4.1	Effects of solar UV radiation on plant responses.....	22
4.1.1	Phenolic metabolites	22
4.1.2	Chlorophyll.....	26
4.1.3	Carbon, nitrogen and cell wall chemistry in litter.....	27
4.1.4	Plant growth, allometric ratios and leaf anatomy	27
4.2	Effects of solar UV radiation on soil fauna, soil respiration and decomposition.....	28
4.3	Assessment of action spectra	29
4.4	Enhancement errors in UV-B supplementation experiments	31
5	CONCLUSIONS	32
	<i>Acknowledgements</i>	34
	YHTEENVETO (RÉSUMÉ IN FINNISH).....	36
	REFERENCES.....	38

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original articles, which will be referred to in the text by their Roman numerals I-V. I took part in the original planning of the experimental design (all papers except V), performed the majority of experimental work in I, II and III, supervised experimental work in IV, carried out part of the calculations in V, and I was the lead writer of the manuscripts (all papers except V), which were completed in co-operation with the other authors.

- I Kotilainen, T., Tegelberg, R., Julkunen-Tiitto, R., Lindfors, A. & Aphalo, P. J. 2008. Metabolite specific effects of solar UV-A and UV-B on alder and birch leaf phenolics. *Global Change Biology* 14: 1294-1304.
- II Kotilainen, T., Haimi, J., Tegelberg, R., Julkunen-Tiitto, R., Vapaavuori, E. & Aphalo, P. J. 2009. Solar UV radiation alters alder and birch litter chemistry that in turn affects decomposers and soil respiration. *Oecologia* 161: 719-728.
- III Kotilainen, T., Tegelberg, R., Julkunen-Tiitto, R., Lindfors, A., O'Hara, R. B. & Aphalo, P. J. Phenolic metabolites of alder and birch leaves through a growing season with solar UV radiation manipulations. Submitted manuscript.
- IV Kotilainen, T., Venäläinen, T., Tegelberg, R., Lindfors, A., Julkunen-Tiitto, R., Sutinen, S., O'Hara, R. B. & Aphalo, P. J. 2009. Assessment of UV biological spectral weighting functions for phenolic metabolites and growth responses in silver birch seedlings. *Photochemistry and Photobiology* 85: 1346-1355.
- V Kotilainen, T., Lindfors, A., Tegelberg, R., & Aphalo, P. J. Outdoors UV-B supplementation with lamps and its relation to ozone depletion: an assessment of enhancement errors. Submitted manuscript.

1 INTRODUCTION

1.1 Stratospheric ozone depletion, climate change and UV-B radiation

The first reports of the ozone hole over Antarctica were published in the mid-1980s (Farman et al. 1985), which were followed by reports of spring-time ozone depletion over the Arctic in the 1990s (von der Gathen et al. 1995). Only the shortest wavelengths of the solar spectrum at ground level are affected by the ozone layer, i.e. the UV-B band (280-315 nm), and it has very little effect on the amount of UV-A radiation reaching ground (315-400 nm) (Mazza et al. 2000). The potential harmfulness of increased UV-B radiation is due to the energy possessed by one photon, which is wavelength dependent; the shorter the wavelength, the more energy there is per mole of photons. Enhanced UV-B radiation is of concern because it can damage plant proteins, nucleic acids and other macromolecules (Ballaré et al. 1996, Jansen et al. 1998). Besides ozone, UV-B radiation is influenced by factors such as clouds, air pollution, aerosols and surface reflection and there is normal seasonal and spatial variation in UV-B irradiance (Madronich et al. 1998, McKenzie et al. 2007).

As a result of the Montreal Protocol and its amendments restricting the use of ozone depleting halogens, the recovery of the ozone layer to pre-1980 levels is expected by the mid 21st century at mid-latitudes and a decade or two later in polar regions (McKenzie et al. 2007). However, there are complex interactions between ozone depletion and climate change. Heat retention by greenhouse gases in the troposphere may result in further stratospheric cooling and increased ozone depletion (Shindell et al. 1998, Taalas et al. 2000, McKenzie et al. 2007). Further, recent models predict that climate change will alter the tropospheric ozone budget and consequently the UV flux reaching the ground. The predicted increase in the stratospheric Brewer-Dobson circulation (e.g. McLandress & Shepherd 2009) acts to decrease ozone in the lower stratosphere in the tropics but to increase it at mid-latitudes (Li et al. 2009). In their study Hegglin & Shepherd (2009) predict that global stratosphere-to-troposphere

ozone flux will increase by 23% between 1965 and 2095. In concordance, the clear-sky UV index will decrease by 9% in northern high latitudes but increase by 4% in the tropics, and increase by up to 20% in southern high latitudes in late spring and early summer. In northern high latitudes the effect would be much larger than that of stratospheric ozone recovery, but the latter increase in the UV index is equivalent to nearly half of that generated by the Antarctic ozone hole created by anthropogenic halogens.

1.2 UV radiation and plant responses

Before a light-driven physiological process occurs in plant, that light must be absorbed by a photoreceptor. An absorption spectrum describes the ability of a photoreceptor to absorb light. An action spectrum describes the relative effectiveness of energy at different wavelengths in producing a biological response. Action spectra are derived by action spectroscopy (McDonald 2003, Björn 2007). The response of the system is analysed quantitatively as a function of wavelength of light and the resulting action spectrum is a measure of the relative efficiency of light of different wavelengths in inducing a defined effect on the examined system (Ghetti et al. 2006). One of the best known photobiological processes in plants is photosynthesis: similarity of the absorption spectrum of chlorophyll and the action spectrum of photosynthesis tells us that chlorophylls are the most important pigments in the process. The spectra are not identical though, because there are also other pigments, e.g. carotenoids, which play a role as well (McDonald 2003, Björn 2007).

Plants adjust their developmental processes, e.g. seed germination, stem elongation and circadian rhythms, according to light signals perceived through different photoreceptors. Phytochromes sense red/far-red radiation and cryptochromes and phototropins sense blue/UV-A radiation (Batschauer 1998). The molecular and spectral characterisation of these light sensors and signal transduction are well established (e.g. Batschauer 1998, Chen et al. 2004, Jiao et al. 2007). Photoreceptors can receive both the energy and information contained in the absorbed light (Björn 2007). Multiple photoreceptors with interactive pathways are the source of flexibility for a versatile system plants need in order to efficiently respond to the light signals (Casal 2000). Signals perceived by a plant through photoreceptors can affect whole plant success, e.g. phytochromes (through perception of red to far-red ratio of sunlight, which changes due to the proximity of neighbouring plants) have been suggested to act as central organizers of the overall resource allocation strategy of plants (Ballaré 2009).

There are numerous studies concerning the effects of increasing UV-B radiation on different plant responses and with different plant species (for a review see Searles et al. 2001). Concerning plant growth, in general studies with UV-B supplementation or attenuation have demonstrated some small effects on e.g. plant height (Caldwell et al. 2007), root biomass and root:shoot ratio (de la Rosa et al. 2003, Rinnan et al. 2005) and leaf anatomical features (e.g. Kostina et

al. 2001). Besides being potentially harmful, plants also show photomorphogenic responses to ambient levels of UV-B radiation (Suesslin & Frohnmeyer 2003, Ulm & Nagy 2005). However, the underlying mechanisms of UV-B perception are still very poorly understood. Interactions between the well defined photoreceptors as well as new ones are suggested to have a role in UV-B perception. For example, low doses of UV-B, perceived by a receptor system different from phytochromes, cryptochromes, or DNA, enhance a de-etiolation response in *Arabidopsis* seedlings, which is induced by active phytochrome B (Boccalandro et al. 2001). Brown et al. (2005) have reported that UV-B may be perceived by a novel class of UV-B-specific signalling component, in a similar way as *Arabidopsis* protein UVR8, which regulates expression of a range of genes essential for UV-B protection.

Plants protect themselves from UV-B radiation by modifying leaf anatomy, e.g. by thicker upper epidermis and spongy parenchyma (Kostina 2001) and also by epidermal wax and leaf hairs, that scatter and reflect radiation (e.g. Vogelmann 1993, Kinnunen et al. 2001). Production of phenolic compounds, in particular flavonoids that accumulate in leaf epidermal cells and absorb UV-B radiation, protecting sensitive processes in mesophyll cells, is the most efficient mechanism to guard against UV-B radiation (e.g. Li et al. 1993, Landry et al. 1995, Lavola 1998a, Bornman 1999). Consequently, production of phenolic compounds is the most common response to enhanced UV-B radiation reported in field studies (Searles et al. 2001, Bassman 2004). However, the bulk production of phenolics is not the only measure of photoprotection, since UV-B induces the synthesis/accumulation of some, but not necessarily all phenolic compounds, as shown in studies with supplemental UV-B radiation with *Betula pendula* (Lavola et al. 1997, de la Rosa et al. 2001, Tegelberg et al. 2001). Moreover, exclusion studies using filters absorbing UV-A and UV-B radiation with *Pinus sylvestris* have demonstrated that the concentration of phenolic compounds responded mainly to UV-A in the field (Turunen et al. 1999, Martz et al. 2007).

In addition to their role in UV protection, quercetin and its glycosides (flavonoids) and chlorogenic acids have been shown to be effective antioxidants (e.g. Appel 1993). In a UV-B supplementation study with silver birch seedlings strong negative correlations were found between concentrations of quercetin and apigenin and lipid peroxidation, indicating an antioxidant role of secondary metabolites in birch leaves (Kostina et al. 2001). Further affecting their ability to protect plant tissues from radiation is the chemical reactivity of phenolics, which can increase due to e.g. air pollutants and UV-B radiation (Appel 1993), as suggested in a study with willows and silver birch (Lavola 1998b).

1.3 Effects of UV radiation on terrestrial ecosystems

It has been speculated that despite subtle changes in individual plants exposed to UV-B radiation, the most important effects of enhanced UV-B radiation would be apparent at the ecosystem level, through interactions over multiple trophic levels (Paul et al. 1997, Day & Neale 2002, Paul & Gwynn-Jones 2003). Secondary metabolites are ideal candidates for mediating multiple trophic responses to UV-B radiation, affecting interactions between plants and herbivores, nutrient cycling and other ecosystem-level processes (e.g. Rozema et al. 1999, Bassman 2004, Zepp et al. 2007). Secondary metabolites can be used to demonstrate cause and effect mechanisms, since their induction can be monitored from the molecular/photochemistry level through to effects on higher trophic levels (Bassman 2004). However, our knowledge about the ecological roles and the overall impacts of both UV-A and UV-B radiation on terrestrial ecosystems is still limited.

Nutrient cycling, i.e. nutrient mineralization from dead organic matter by soil microbes, determines the availability of nutrients to plants in many ecosystems, including boreal forests (van der Heijden et al. 2008). Furthermore, nutrient release via physical and, to a lesser extent, chemical modification of the decomposing material and the soil environment is affected by litter consumers, microarthropods and some macrofauna (Bardgett 2005). Species-specific production of phenolic compounds could have a bearing on soil microbial activity and nutrient cycling at the ecosystem scale, further having an effect on competitive interactions of plants (Bardgett 2005). In particular, tannins in plant litter may have an important role in plant-litter-soil interactions. The primary influence of tannins on ecosystem functioning is suggested to be due to their impacts on nutrient dynamics. Tannins may alter N cycling by e.g. hindering decomposition rates and inhibiting enzyme activities and, as a result, reduce nutrient losses in infertile ecosystems. Function and metabolism of soil organisms such as nematodes, arthropods, enchytraeids and earthworms may also be inhibited by tannins (Kraus et al. 2003).

The effects of UV-B radiation through plants on soil organisms and decomposition processes have been well acknowledged (Caldwell et al. 2007). Convey et al. (2002) have also reported impacts of UV-A radiation on soil microbes and microinvertebrates in exclusion studies. Indirect effects on decomposition may stem from changes in plant chemistry induced by UV radiation during plant growth. Changes induced by UV radiation can affect the factors which are considered to have an important role in the decomposition of litter (e.g. concentrations of lignin, nitrogen and carbohydrates and e.g. the ratios of lignin:nitrogen and C:N) (Paul et al. 1999). Hence, benign effects of UV-B radiation on plants can still magnify the effects of stratospheric ozone depletion through indirect effects on decomposers (Johnson et al. 2002, Pancotto et al. 2003).

1.4 Tackling the problem of varying spectra from the sun compared to UV lamps

Action spectra available for plant responses to UV radiation predict different slopes for the relationship between ozone depletion and the increase in effective UV radiation at ground level. This slope is usually described by a single number, the radiation amplification factor (RAF) (Flint & Caldwell 2003a). The estimated value of RAF will depend on the action spectrum used, and this should be chosen according to the biological response under consideration.

In experimental work problems inherent with calculation of UV doses relate to differences between spectra of UV lamps and in solar spectra following the changes in the ozone column (Mazza et al. 2000, Flint & Caldwell 2003a, 2003b). In order to overcome the problem of differing spectral output, supplemental UV doses are calculated using action spectra as biological spectral weighting functions (BSWFs) (Flint & Caldwell 2003a, 2003b). Characteristics of BSWF will play a large role in the amount of radiant flux that should be delivered by lamp systems in experiments. Certain UV-B flux from lamps can be demonstrated to specifically elicit plant effects, but it still does not necessarily mean that the response is significant concerning the ozone reduction problem. Based on spectral criteria, the supplied UV-B dose used in experiments may be over- or underestimated (Caldwell & Flint 1997). Other important factors possibly leading to misinterpretation of the results are excessive supplementation of UV-B radiation when weather conditions (clouds) decrease solar UV-B irradiance or when there is shading by the lamp frames (Flint et al. 2003).

A complication when using the BSWF is that the action spectra are different for different plant processes (Caldwell et al. 2007, Sullivan et al. 2007). The relationship between the required daily burning time of lamps and the level of ozone depletion targeted in experiments depends on the action spectrum assumed to rule the phenomenon studied. Consequently, because different processes in the plant follow different action spectra in their response to UV, these different processes will be subjected to different simulated levels of ozone depletion.

Usually action spectra are derived using monochromatic light fluxes at different wavelengths and by demonstrating a direct photochemical effect on a specific target. In order to study the complex network of responses, plant experiments have to be carried out with the application of a polychromatic spectrum, in which UV-B, UV-A and PAR are present in the same proportions as in outdoor global radiation and in which additional UV-B radiation can be modified. As these demands are difficult to realise in experimental conditions, especially when dealing with intact plants, only a few action spectra based on polychromatic irradiations have been described (Ibdah et al. 2002, Ghetti et al. 2006).

The most commonly used BSWFs for experiments with terrestrial plants have been the generalized plant action spectrum and its formulations, which are composites of nine different UV-B responses (not including plant growth responses) (Caldwell 1971). Also other BSWFs have been used, with varying responsiveness from the UV-B region towards increasing wavelength in the UV-A region (Flint & Caldwell 2003a, Flint et al. 2004). I had eight different BSWF under focus in my studies. GEN(G) is the most commonly used formulation of the generalized plant action spectrum (Green et al. 1974) and GEN(T) is another formulation of the same generalized plant action spectrum (Thimijan et al. 1978). CIE is an action spectrum for ultraviolet induced erythema in human skin (standardized by the International Commission on Illumination) (McKinlay & Diffey 1987). DNA(P) is the action spectrum by Quate et al. (1992) as formulated by Musil (1995), for intact plant DNA damage in alfalfa (*Medicago sativa*) seedlings. DNA(N) is the action spectrum for "naked" DNA damage by Setlow (1974). PHIN is a spectrum for photoinhibited reactions in isolated chloroplasts (Jones & Kok 1966). PG is a spectrum measured for growth responses in oat (*Avena sativa*) (Flint & Caldwell 2003a). FLAV is a polychromatic spectrum for the accumulation of a flavonol in *Mesembryanthemum crystallinum* (Ibdah et al. 2002). For details of these spectra, see IV and V.

The use of different BSWFs can partly explain the varying results of different experiments. Assessing the appropriateness of action spectra used in field conditions is suggested to be a critical step in testing biological spectral weighting functions for plant responses (Caldwell & Flint 1997, Caldwell et al. 2007). Difficulties related to the use of BSWFs count heavily in the conduct and evaluation of experiments designed to assess plant and ecosystem responses to changes in UV radiation. Thus careful testing of the BSWFs and further, simultaneous testing for multiple plant responses is required to fully assess the UV-B-dependent effects of stratospheric ozone depletion on plants and consequential implications at other trophic levels.

2 OBJECTIVES

Using an inappropriate action spectrum as a BSWF in experiments concerning stratospheric ozone depletion can lead to too low or too high doses of UV-B compared to the ozone depletion target, which in turn causes misinterpretation of the results of the experiments. Further, focusing on the possible detrimental effects of increased levels of UV-B radiation has detracted focus from the photoecological role of both UV-B and UV-A radiation. My objective in this thesis was to assess the validity of past experiments and to develop new methods and models for assessing the reliability of previous experiments studying the effects of supplemental UV-B radiation. I did this by comparing the responses of three Betulaceae species to varying levels of solar UV-B and UV-A radiation with two field experiments and one outdoor experiment with a factorial setting. In addition, I assessed the effects of litter, grown under different UV regimes, to soil fauna and soil respiration and measured the decomposition rate. Further, I compared the published action spectra used as BSWFs and modelled the level of ozone depletion that the past experiments have actually simulated.

The main hypotheses were:

1. Chemical and physiological responses in plants, including accumulation of individual phenolic metabolites, respond variably to exclusion of solar UV radiation and the responses can be species specific (I-IV).
2. Accumulation of individual phenolic metabolites changes during a growing season and the response to exclusion of solar UV radiation varies (III).
3. Changes in the chemistry of litter, grown under different UV treatments have effects on the responses of soil fauna and soil respiration (II).
4. The appropriateness of a BSWF to predict the accumulation of phenolics varies between individual phenolic metabolites and also during a growing season (III, IV).

5. Differences in the emphasis the BSWFs give to the UV-A band determine the possible differences in their appropriateness for predicting a given response (V).
6. Experimental location and other factors during the experiment, e.g. cloudiness, are important in defining the choice of an appropriate BSWF (V).

3 MATERIALS AND METHODS

3.1 Field experiments (I, III)

3.1.1 General design of the field experiments

Field experiments with trees in an abandoned agricultural field in years 2004 and 2005 were based on the use of plastic films excluding or attenuating different parts of the UV spectrum. For the spectral transmittance properties of the filters, see Fig. 2 in article I. I had two tree species: grey alder (*Alnus incana*) and white birch (*Betula pubescens*), with all treatments on different branches of each tree. The filters were installed before budbreak, during the first week of May in both years and remained on the branches until the end of the growing season. All branches used were on the south facing side of the crown (Fig. 1). Leaf samples for phenolic analyses were collected so that one fully expanded leaf was taken from each branch near the centre of the filter (in field experiment year 2004 in the case of four alder trees with fewer treated branches, two leaves per branch were taken). Variability in phenolic composition among leaves on similar branches of the same tree is typically less than that occurring between trees (Suomela et al. 1995), allowing adjacent samples to be considered equivalent. To avoid taking subsequent samples from the same small branch, the sampling location was marked with a piece of string. This was done to avoid possible changes induced by the sampling, i.e. taking a leaf sample might in plants perspective imitate herbivory, which could consequently contribute to enhanced production of phenolic compounds in adjacent leaves.

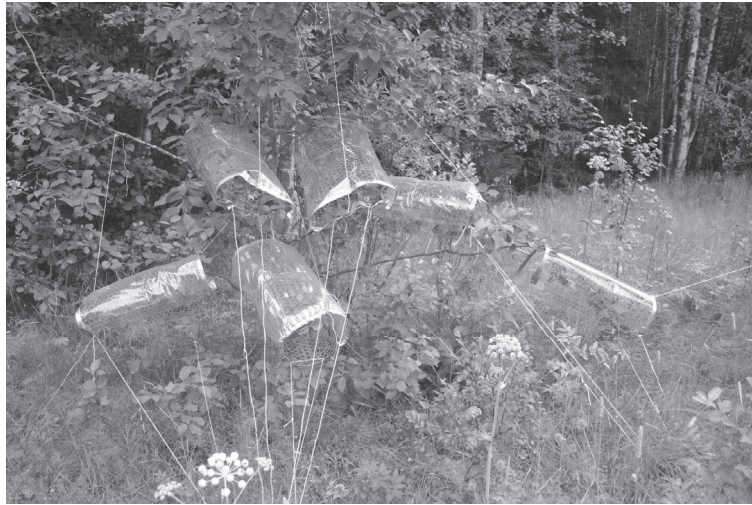


FIGURE 1 Field experiment, one grey alder tree.

3.1.2 Field experiment year 2004 (I)

In year 2004 I had three treatments: polythene for near ambient control (UV-A+, UV-B+), polyester for exclusion of UV-B radiation (UV-A+, UV-B-) and surface dyed polyester (Rosco) for exclusion of both UV-A and UV-B radiation (UV-A-, UV-B-). Leaf samples for phenolic analyses were collected three times during the season.

3.1.3 Field experiment year 2005 (III)

The setup used in 2005 was physically similar to the experiment in 2004, but with more treatments. Intermediate UV treatments were created by combining strips of the different films. For exclusion of half of UV-B I used stripes of polyester over polythene (UV-B 50%, UV-A 100%), exclusion of half of UV-B and half of UV-A treatment (UV-B 50%, UV-A 50%) was created with stripes of surface dyed polyester over polythene and finally all UV-B exclusion combined with exclusion of half of UV-A (UV-B 0%, UV-A 50%) was created with surface dyed polyester over polyester. Film stripes were 15 mm wide and 15 mm apart. Leaf samples for phenolic analyses were collected four times during the season. In addition, leaf samples for chlorophyll analyses were collected in late summer.

3.2 Decomposition experiments (II)

3.2.1 General design of the decomposition experiments

The two decomposition experiments, with soil and litter and with litter and woodlice (*Porcellio scaber*), were conducted under laboratory conditions. I used leaves grown under different UV treatments in the field experiment of year 2004. Leaves (hereafter litter) were collected from the trees when they were near abscission. Litter from each treatment and tree was placed in separate microcosms.

3.2.2 Microcosms with soil and litter

Plastic jars were used as microcosms. The microcosms, with soil (collected from the field experimental site) and litter placed on the surface of the soil, were incubated in a climate chamber (+17 °C) for 18 weeks. We measured litter mass loss during the experiments as well as soil pH from the soil samples at the end of the experiments. Soil animals (nematodes and enchytraeid worms) were extracted from the soil samples and CO₂ production (soil respiration) was measured using appropriate standard methods. To study the long term effects of different UV treatments on litter decomposition, we had another similar experiment that continued for 13 months.

3.2.3 Microcosms with woodlice and litter

Glass jars with casting made of plaster of Paris containing charcoal at the bottom were used as microcosms. The microcosms, with three woodlice and litter were incubated in a climate chamber (+17 °C) for 13 weeks. We measured litter mass loss, CO₂ production and woodlice growth during the experiment. At the end of the experiment, faeces of woodlice were weighed, dried and phenolics were analysed.

3.3 Outdoor experiment (IV)

Treatments in outdoor experiment year 2006 were similar to those of the field experiment in year 2005, described above. Silver birch (*Betula pendula*) seedlings planted in pots were used in the experiment. The experiment had five blocks, with all six treatments included in each block. Under each frame (30 in all) there were 43 seedlings growing individually in pots, arranged in two trays under the center of each filter frame (Fig. 2). The treatment started on 26 of June 2006. The height of eight seedlings per frame (same every time) was measured twice a week during the experiment. Leaf samples for phenolic and chlorophyll

analyses and for anatomical cross sections were collected at the end of the experiment (11 August 2006).



FIGURE 2 Outdoor experiment, silver birch seedlings under a frame.

3.4 Modelling experiment (V)

For the modelling experiment (V) solar radiation spectra at Jokioinen (60°49'N, 23°30'E) and Sodankylä (67°22'N, 26°38'E) were simulated according to a method presented in Lindfors et al. (2009), for 21 May and 21 June 2000. Calculations were done at hourly time intervals and 1 nm wavelength intervals from 293 to 800 nm, assuming three different cases of cloudiness. Each simulated daily solar spectrum was convoluted by each of the eight action spectra with contrasting effectiveness in the UV region.

The required daily burning time of the lamps was calculated from the lamp emission spectrum from a pair of UV-B lamps (Q-Panel UVB-313, Q-Lab, Cleveland, Ohio, USA) with a cellulose acetate filter (0.115 mm thick) mounted horizontally 25 cm below the lamps. Based on the absolute increase in effective UV due to ozone depletion and the effective UV emission of the lamps, the required daily burning time of the lamps needed to achieve an increase in effective UV irradiance equivalent to that under 10% and 20% ozone depletion was calculated for each of the eight action spectra.

To assess the effectiveness of radiation from lamps compared to that arising from ozone depletion in the modelling experiment (V), solar radiation spectra were estimated for two days at Jokioinen and Sodankylä. The calculations were done at hourly intervals and 1 nm intervals from 293 to 800 nm, according to the method presented in Lindfors et al. (2009). Further, the radiation spectra were simulated assuming three different cases of cloudiness

(heavy clouds throughout the day or light clouds in the morning & moderately thick clouds during the rest of the day or clear sky) and three different values for ozone; the normal climatological value and values simulating 10 and 20 % ozone depletion. This gives the effect of ozone depletion on solar radiation. To compare this to the emission spectrum of the UV-B lamps, both the difference spectrum for the effect of 10 or 20% ozone depletion on solar UV and the filtered UV-B lamp emission spectrum were standardized to total energy in the UV range. These standardized spectra were multiplied by each of the action spectra in turn and the result was integrated over the wavelength range from 293 nm to 400 nm. Finally an effectiveness ratio comparing the solar radiation to the radiation resulting from UV-B lamps was calculated.

3.5 Analyses

3.5.1 Chemical analyses and plant growth measurements

Tannins and individual phenolics were measured from the leaf and litter samples collected from both field experiments (I-III) and from the leaf samples collected from the outdoor experiment (IV). After collecting the leaf samples, they were dried in a ventilated oven (+30°C, five days) and then stored at -20°C. Tannins were analysed with a butanol-HCl test (Hagerman 1995) and recording the absorbance with a spectrophotometer at 550 nm. Tannin tests were standardized with purified tannin either from leaves and litter of *A. incana* or *B. pubescens* collected from the trees in the field experiment (I, II, III) or leaves of *B. pendula* collected from the seedlings in the outdoor experiment (IV). Individual phenolics were analysed with HPLC. The HPLC-DAD analyses were performed with an Agilent 1100 Series (Waldbronn, Germany) as described in Keinänen & Julkunen-Tiitto (1998). Retention times and UV spectra were used to identify the compounds monitored at 220, 270, 320 and 360 nm. Compound identification is described in Keinänen & Julkunen-Tiitto (1998) and Keski-Saari et al. (2005). The accuracy of the measurement of individual phenolics was confirmed with replicate samples analysed from leaves collected from the field experiment 2005. The variation between the replicate samples of summed phenolics was on average 5,4 % in alder leaves and 7,1 % in birch leaves (data not shown).

From the litter samples collected from the field experiment 2004 (II) carbon and nitrogen was also measured. Part of the litter collected, remaining after initial sampling for phenolics analyses, was ground to a fine powder using a mill. Carbon and nitrogen were analysed from the powder with an element analyzer (EA 1110 CHNS-O, CE Instruments, Milan, Italy). The same milled litter was analysed to determine litter cell wall composition for lignin, total hydrolyzable sugars, α -cellulose and uronic acid concentrations using standard extraction methods. Different phenolics and carbon and nitrogen content were also analysed from the woodlice faeces (II).

Chlorophyll concentrations were measured from fresh leaf samples collected from both field experiment 2005 and the outdoor experiment (III, IV). The concentrations were estimated by measuring absorbance with a spectrophotometer at 750, 663.8 and 646.8 nm and using the extinction coefficients from Porra et al. (1989).

CO₂ production (soil respiration) was measured in the decomposition experiments (II) with an infrared carbon analyzer (EQ 92 Universal Carbon Analyzer, PPM Systems, Espoo, Finland). In the decomposition experiment with soil and litter, CO₂ production was measured 13 times. The litter was weighed (f.m.) every other week, nine times in all. At the end of the experiment, the leaf litter was dried and weighed (d.m.). Soil pH was measured and nematodes and enchytraeids were extracted using wet funnel methods (O'Connor 1962, Sohlenius 1979). At the end of the long-term decomposition experiment, the same procedures were applied. In the decomposition experiment with woodlice and litter, CO₂ production was measured 12 times during the experiment. The litter (f.m.) and the woodlice were weighed twice a month, six times in all. At the end of the experiment litter was dried and weighed (d.m.) and woodlice were weighed. In addition, faeces of woodlice were dried and weighed (d.m.).

From the leaf samples collected from the outdoor experiment (III) growth of the seedlings and number of leaves were measured. In addition, samples for anatomical cross sections were taken. Fixation, staining and preparation were done as in Kivimäenpää et al. (2004). The light microscopy samples were measured for e.g. total leaf thickness, palisade and spongy layer thickness and number of hairs and vascular bundles.

3.5.2 Data analyses

The data of individual phenolic metabolites from the field experiments (I, III), decomposition experiment (II) and outdoor experiment (IV) were analysed by fitting a linear mixed effects model. The data of soil respiration and responses of the soil fauna from the decomposition experiment (II) were analysed similarly. Analysis was performed with R software (R Development Core Team 2006), using package NLME (Pinheiro & Bates 2000). Transformations of the data were not used, but a power of variance function covariate was included in the model in cases when variances were not homogeneous, as revealed by a likelihood ratio test between models. Normality was checked with quantile-quantile plots of residuals. For discussion of results $\alpha = 0.05$ was used as the limit for significance of main effects and interaction. A more stringent condition was used for testing whether there was an effect of the UV treatments. Once an effect had been demonstrated, a weaker test was used to try to identify whether this effect could be attributed to UV-A, UV-B or both, therefore for the effects of UV-A or UV-B radiation $\alpha = 0.10$ was used. With the outdoor experiment (IV), data were first subjected to multivariate analysis of variance (MANOVA), separately for 1) all primary growth measurements, 2) individual phenolic

metabolites, 3) chlorophylls and 4) primary anatomical measurements. Fittings of linear mixed effects models were done only if an overall significant effect of treatments was detected by MANOVA.

To assess the suitability of the action spectra in field experiment 2005 (III) and in the outdoor experiment (IV) we estimated the mean effective UV doses ($\text{kJ m}^{-2} \text{d}^{-1}$) for the duration of the experiment, according to the method presented in Lindfors et al. (2009). Estimates were then convoluted with measured filter transmittance and six different action spectra. The difference in plant response between the two most extreme treatments, near ambient control (maximum UV-B and UV-A) versus attenuated UV (minimum UV-B and UV-A) was calculated. This difference was then partitioned among the remaining intermediate treatments as a proportion of the total response. Standard errors and 95 % confidence intervals were calculated using a parametric bootstrap. For computing the predicted effect for each BSWF under each radiation regime, the estimated effective doses calculated using the different BSWFs were treated in a similar manner as the plant responses. Plant response for each intermediate treatment was then compared with the response predicted by the different BSWFs. The confidence intervals were used to test for the significance of differences between observed relative responses and expected responses. The expected responses were compared to the observed ones only if the test of significance for overall treatment effect on phenolic concentrations yielded $p < 0.05$. The method used in the current experiment allows us to reject action spectra at a 5 % significance level. However, in an absolute sense it can not be stated that the spectra not rejected are equally good as predictors, since the experimental evidence is not strong enough to allow distinguishing the best action spectrum at predicting the studied response.

4 RESULTS AND DISCUSSION

4.1 Effects of solar UV radiation on plant responses

4.1.1 Phenolic metabolites

All phenolic groups, except for phenolic acids and presumed stilbenes measured only from grey alder leaves, were variably affected by the UV treatments (Table 1). In my studies, there was variation in the direction of the UV-A or UV-B effect. Sometimes these two UV bands had an effect in the same direction, e.g. flavonoids in silver birch (IV), and in other cases there was variation in the linearity of the response to UV-B or UV-A, e.g. for chlorogenic acids in grey alder there was a linear UV-B effect and both linear and quadratic UV-A effect (III, Table 1). This means that in addition to the linear effect and the concentration increasing from ambient UV-A to all UV-A exclusion there was also a quadratic component in the response: the concentration of chlorogenic acids increased more after half UV-A exclusion to all UV-A exclusion than it did after ambient UV-A to half UV-A exclusion.

Flavonoids have been shown to respond effectively to UV radiation (Lavola et al. 1997, Lavola 1998a, de la Rosa et al. 2001, Tegelberg et al. 2001) and their role as plant “sunscreens” is further confirmed in my studies (I-IV). However, even within the group flavonoids the individual metabolites responded differently to the UV treatments (I, III, IV). Moreover, the accumulation of chlorogenic acids changed in response to UV exclusion, but unlike most flavonoids, which mainly decreased in concentration along with UV exclusion, the concentration of chlorogenic acids had a tendency to increase. This suggests some other role, besides UV protection, for chlorogenic acids.

Interestingly, it seems that differences in leaf senescence, (alder leaves drop while still green, whereas birch leaves first become yellow), is reflected in the litter phenolic profiles. In general, the effects of UV radiation were similar in both green leaves and litter in alder (I, II). In contrast, in birch the concentrations of chlorogenic acids and flavonoids were affected by the UV

TABLE 1 Responses of phenolic metabolites by compound group in different experiments. uvA = statistically significant UV-A effect, uvB = statistically significant UV-B effect, x = no statistically significant UV effect, - = metabolites belonging to the group not detected. Additionally, in the field experiment in year 2005 and in the outdoor experiment (III, IV) superscript letter "l" denotes a linear effect and "q" denotes a quadratic effect. Summed phenolics 1 = summed phenolics without condensed tannins, summed phenolics 2 = summed phenolics with condensed tannins. * In alder, in phenolic glycosides and summed phenolics with condensed tannins in the field experiment in year 2004 (I) there was an interaction between treatment and sampling time and the UV effect was observed in the second sampling. In summed phenolics without tannins there was also interaction between treatment and sampling time, but no statistically significant UV effect could be detected in any of the three samplings. In birch in summed phenolics without condensed tannins in the field experiment in year 2004 (I) there was interaction between treatment and sampling time and the UV effect was observed in the first sampling. well.

Group	<i>A. incana</i>		<i>B. pubescens</i>		<i>B. pendula</i>
	I	III	I	III	IV
Phenolic acids	x	x	-	-	-
Cinnamic acids	uvA	uvB ^q , uvA ^{lq}	-	x	x
Phenolic glycosides	uvB*	x	-	-	x
Chlorogenic acids	uvB, uvA	uvB ^q , uvA ^{lq}	uvB, uvA	uvA ^l	uvB ^l
Flavonoids	uvB, uvA	uvB ^{lq}	uvB	uvB ^l , uvA ^q	uvB ^l , uvA ^l
Hydrolyzable tannins	-	-	-	uvA ^q	-
Presumed stilbenes	x	x	-	-	-
Summed phenolics 1	x*	x	uvB, uvA*	x	uvB ^l
Condensed tannins	x	uvB ^l , uvA ^{lq}	x	x	uvB ^l
Summed phenolics 2	uvB*	x	x	x	uvB ^l , uvA ^l

treatments, when measured from green leaves (I), but not when measured from litter (II).

When considering this variability, it has to be kept in mind that these groups are composed of different metabolites in the two tree species and to some extent even within one species between experiments. There are of course differences in the experimental setup between years, and the differences in the concentrations of condensed tannins and consequently in summed phenolics between the two field experiments result from the differences in analyses. Condensed tannins in year 2004 were measured from both extract and the residue left at the stage when the supernatant was collected. In year 2005 this residue was not tested for tannins simply because of the overwhelming amount of samples.

Presumably the main cause of variation is the plasticity inherent in the phenolic accumulation and the multiple factors affecting the accumulation of phenolic metabolites. The qualitative composition of foliar phenolics is

controlled mainly by genotype. However, the quantitative chemical variation is controlled by seasonal changes in the environment, e.g. water and nutrient availability, shading, herbivory and UV radiation (e.g. Waterman & Mole 1994, Jones & Hartley 1999, Sullivan et al. 2007). Moreover, the differences between responses in this thesis and previous experiments can relate in part to the fact that several photoreceptors and the absorption of radiation by a multitude of biomolecules trigger the changes mediating a number of light responses (Casal 2000, Brosche & Strid 2003). In concordance, there are results indicating that longer wavelength UV-B responses appear to be photoregulatory rather than resulting from damage or stress and that there are multiple signalling components, including integrated UV-A/blue and UV-B signalling pathways acting together in a photoregulatory pathway (Jenkins et al. 2001, Brown et al. 2005, Brown & Jenkins 2008). In light of the findings of my studies, summed concentration of phenolics, i.e. measuring phenolics only as crude extracts, can be misleading. While the concentrations of individual metabolites may change, summed concentration does not necessarily change, which does not indicate that there are no changes in UV protection. In birch, condensed tannins have been shown to have low efficiency in absorbing UV-B radiation and hence they are not sensitive to UV-B radiation (Tegelberg et al. 2001). Similarly, it has been reported that the use of phenolic absorbance to estimate true epidermal screening is restricted by optical heterogeneity and variable distribution of phenolics (Kolb & Pfündel 2005).

Despite the fact that not all phenolics measured responded to UV treatments, all the phenolic groups in both tree species used in the field experiments, (with the exception of presumed stilbenes in alder and condensed tannins in birch in field experiment 2004), showed clear variation during the season (Fig. 3 & Fig. 4) (I, III). Flavonoids, chlorogenic acids and cinnamic acids in both tree species showed similar patterns during the season in both field experiments: concentrations were highest in early summer, decreasing at the second sampling and remaining at that level or decreasing slightly later in the season. Also hydrolyzable tannins and summed phenolics without condensed tannins measured in birch in field experiment year 2005 showed a similar pattern. These results are in agreement with earlier findings from experiments with different birch species (Ossipov et al. 1997, Salminen et al. 2001, Laitinen et al. 2002, Riipi et al. 2002, Haukioja 2005). However, the concentration of phenolic acids, phenolic glycosides, presumed stilbenes and summed phenolics without condensed tannins in alder varied between the two years.

Possible factors responsible for seasonal variation in the concentrations of phenolic metabolites vary from the dilution effect, the increase in dry mass during leaf expansion is supposed to result in dilution of phenolics synthesized at the bud stage (Jones & Hartley 1999), to changes in abiotic factors like temperature (Bilger et al. 2007, Olsen et al. 2009) and also could be related to developmental processes (Liakoura et al. 2001). The estimated total irradiance (UV+PAR) during the second field experiment (III) shows a pattern that does not inclusively match the responses of the phenolic groups. However, Sullivan

et al. (2007) found a correlation between changes in UV-screening compounds and short-term changes in ambient UV levels. Nevertheless, the sensitivity of the responses of the two species studied (*Hordeum vulgare* and *Glycine max*) varied (Sullivan et al. 2007).

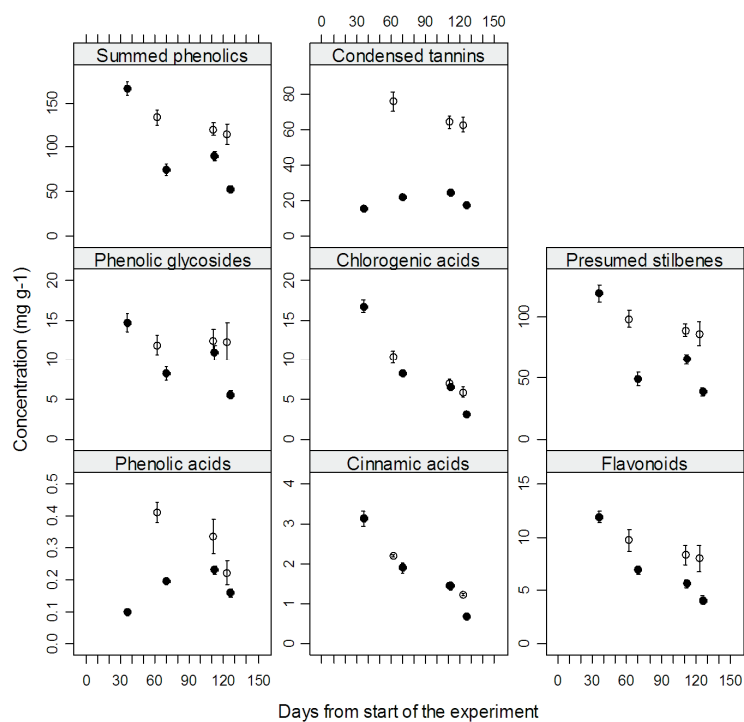


FIGURE 3 Responses of phenolic groups in grey alder during the experiments, averages over all treatments. Both experiments started in the first week of May. Open circles = field experiment 2004 (I), filled circles = field experiment 2005 (II). Sampling dates for field experiment 2004 were 7th of July, 25th of August and when the leaves were ready for abscission, between 6th of September and 10th of October. For field experiment 2005 the dates were 7th of June, 11th of July, 22nd of August and finally between 5th and 30th of September. Summed phenolics is the concentration of all phenolics except condensed tannins that were measured differently in year 2004 and 2005 (see above).

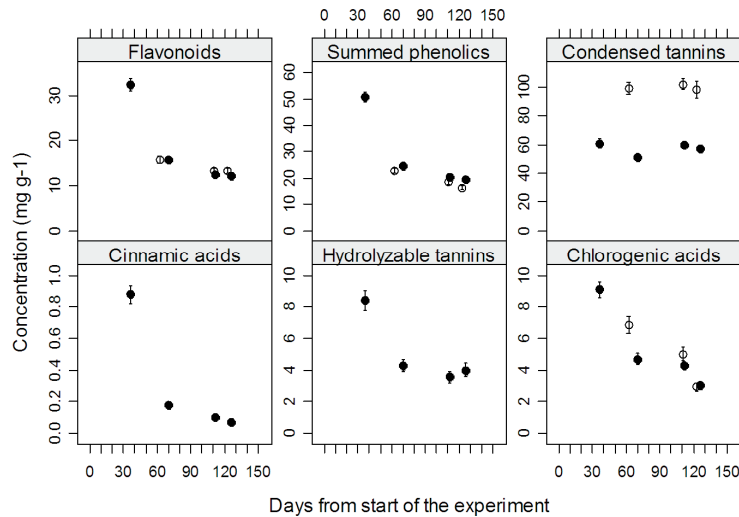


FIGURE 4 Responses of phenolic groups in white birch during the experiments, averages over all treatments. Open circles = field experiment 2004 (I), filled circles = field experiment 2005 (III). See legend to Fig. 3 for details.

Taken together, my results show that different phenolic metabolites responded differently to UV radiation and additionally showed different seasonal dynamics. In addition, there were cases where there was interaction between treatment and sample time (I, III). The temporal responses of the phenolic groups were in many cases similar between the two years in the field experiments (I, III), e.g. in flavonoids and chlorogenic acids in both tree species. However, in grey alder many of the phenolic groups showed variation in their seasonal dynamics between the two years, and in white birch cinnamic acids and hydrolyzable tannins were detected only in year 2005. This provides further evidence that production of phenolic metabolites in the leaves of deciduous trees is mainly controlled by the genotype, but that there is also considerable phenotypic plasticity involved (Lavola 1998b, Tegelberg 2002).

4.1.2 Chlorophyll

Leaf samples for chlorophyll analyses were collected from grey alder and white birch in the second field experiment (III) and from silver birch in the outdoor experiment (IV). Concentrations of chlorophyll consistently were not affected by UV exclusion in both of the experiments and in all of the three tree species. Our results are supported by previous experiments with supplemental UV-B with silver birch seedlings (Tegelberg et al. 2001, Aphalo et al. 2009) and with five other deciduous tree species (*Fraxinus excelsior*, *B. pendula*, *Tilia cordata*, *Quercus robur* and *Acer pseudoplatanus*) (Keiller & Holmes 2001), suggesting a negligible effect of UV radiation on chlorophyll concentrations.

4.1.3 Carbon, nitrogen and cell wall chemistry in litter

Litter collected from the first field experiment was used for the decomposition experiments and litter analyses (II). Exclusion of UV-A affected negatively the percentage of acid soluble lignin, and exclusion of UV-B radiation affected total lignin:α-cellulose ratio in alder litter. In both tree species, exclusion of UV-B affected negatively the total lignin:total hydrolyzable sugars ratio. Opposite effects of UV-B and UV-A were demonstrated with the carbon concentration. In contrast, a experiment with *Gunnera magellanica* showed that UV-B attenuation during growth did not have any significant effects on litter quality (Pancotto et al. 2003). However, an experiment with *Hordeum vulgare* showed variable responses to UV-B exclusion; e.g. the concentrations of cellulose and lignin:N ratio decreased, but the concentrations of N and soluble carbohydrates increased and finally lignin content and C:N ratio were not affected by UV-B exclusion (Pancotto et al. 2005). Species-specific responses to UV radiation and differences in experimental methods likely explain the discrepancy in these results.

4.1.4 Plant growth, allometric ratios and leaf anatomy

In the outdoor experiment (IV) the results on growth parameters, allometric ratios or leaf anatomical features measured from silver birch seedlings did not show any significant response to UV exclusion. In contrast, in a UV-B supplementation study increased levels of UV-B were reported to cause changes in leaf anatomy. Changes varied from increased thickness of palisade parenchyma in leaves of *Populus trichocarpa* and *Quercus rubra* to increased cross-sectional area, thickness and width in needles of *Pseudotsuga menziesii* and finally to increased thickness of the first hypodermis of *Pinus ponderosa* (Nagel et al. 1998). Another study with three-year-old silver birch seedlings showed increased leaf thickness and spongy intercellular spaces in leaves under elevated UV-B radiation, but enhanced UV-B radiation had no significant effects on height growth, and shoot and root biomass of birch seedlings (Kostina et al. 2001). However, in an outdoor experiment with supplemental UV-B radiation, changes in silver birch growth appeared during the third growing season (Tegelberg et al. 2001). Further, growth as measured by height in *Avena sativa* and *Brassica rapa* has been shown to respond to solar UV-A radiation (Flint & Caldwell 2003b). UV induced effects related to growth and leaf anatomy are suggested to be species-specific (Julkunen-Tiitto et al. 2005) and there also seems to be differences in responses to UV radiation between fast-growing herbaceous plants and slow-growing trees. In their review, Rozema et al. (2005) concluded that enhanced UV-B radiation appears to deliver photomorphogenic responses that affect carbon partitioning and allocation, rather than causing significant reductions in growth or biomass accumulation.

4.2 Effects of solar UV radiation on soil fauna, soil respiration and decomposition

Woodlice growth, the amount of litter consumed by woodlice and CO₂ production of the microcosms with litter and woodlice were not affected by the UV treatments (II). However, woodlice grew better when fed with alder litter, likely due to the fact that *P. scaber* grow better when feeding on litter with a lower C:N ratio (Zimmer & Topp 2000). In addition, abundances of nematodes and enchytraeids were not affected by the UV treatments or the tree species. Rotifers, nematodes and mites have been shown to be less abundant under near-ambient UV-B, whereas testate amoebae are more abundant under near-ambient UV-B than under reduced UV-B (Robson et al. 2005). Exposure to near-ambient levels of UV radiation, with separate significant effects for both UV-A and UV-B, decreased numbers of Collembola (Convey et al. 2002). Again, the variable results may stem from the differences in both experimental set-ups and duration.

Further, CO₂ production (assumed to be mainly the result of soil microbial respiration) of the microcosms with soil and litter was lower in soil with litter produced under exclusion of both UV-A and UV-B radiation when compared to soil with control litter for both tree species. In addition to microbes, soil respiration is produced by other heterotrophic organisms and by respiration of living roots and is affected by temperature, moisture and substrate properties. There is evidence that even subtle changes in vegetation induced by UV-B radiation can affect microbial community composition (Rinnan et al. 2005) and microbial biomass C:N ratio (Johnson et al. 2002). Soil-to-atmosphere CO₂ flux is the dominant terrestrial source of CO₂, approximated to be ~10% of the atmosphere's CO₂, which cycles through soils each year (Raich & Tufekcioglu 2000, Raich et al. 2002). Therefore, despite the fact that the UV induced effect on soil respiration in our studies was moderate, it could have a bearing in the planetary carbon cycle as a whole.

The decomposition rates of the litter in the decomposition experiment with woodlice and litter were similar between the two tree species (II). Accordingly, changes in litter chemistry had no influence on the litter mass loss either in the short- or in the long-term decomposition experiment with soil and litter. This is interesting, since beyond the UV effects, there were many differences in the litter chemistry between the tree species (e.g. percentages of nitrogen, carbon and acid soluble lignin were higher in alder compared with birch and *vice versa* with e.g. percentages of α -cellulose, gravimetric lignin and the C:N ratio. Relative importance of factors affecting decomposition rate, e.g. proportion of lignin, phenolic compounds and the ratio of nutrients to carbon, are not fully understood (Bardgett 2005). Further, full decomposition of plant leaves and nutrient recycling is a slow process, taking approximately three years in the tropics, and up to 100 years in the Arctic (Bardgett 2005). Hence, the relatively short duration of the decomposition experiments can explain why the

many differences between species in litter chemistry did not affect the decomposition rate.

4.3 Assessment of action spectra

Comparison of the six action spectra (out of eight published action spectra presented in the Introduction) to the experimental results showed variation between the tree species and phenolic groups and through the growing season in field experiment year 2005. In grey alder, for the experimental responses of flavonoids as a group GEN(G), GEN(T), and PG were rejected at the 5% risk level. The results were further variable for the individual flavonoids and there was variation even between samplings. Results from the field experiment suggest that DNA(P), CIE and FLA(V) were better at predicting the responses in alder than GEN(G), GEN(T) and PG, which were rejected more often (Table 2).

The situation is slightly different in white birch, where there were not so clear differences between the spectra among different flavonoids (Table 2). Interestingly, in white birch all of the six action spectra could be rejected for flavonoids as a group. However, similarly to grey alder, there was variation even between samplings. In the outdoor experiment with silver birch seedlings, with the exception of chlorogenic acid, of the six spectra tested, DNA(P), CIE and FLAV, seemed to give the best match to the observed responses in accumulation of phenolics (IV, Table 2). These findings are supported by findings in an experiment that combined UV-B supplementation with filtering of solar UV-A, accompanied by another experiment selectively filtering solar UV. Measured accumulation of UV-absorbing compounds (measured as crude extracts) in leaf tissue of *Avena sativa*, *Kochia scoparia*, *Capsicum annuum* and *Sorghum bicolor* showed that BSWF that extend into the UV-A region with moderate effectiveness, such as DNA(P) and FLAV, best represented the observed results (Flint et al. 2004). Sullivan et al. (2007) suggested that response differences to UV radiation between plant species were due to the unique composition of phenolic compounds and following this, response estimates or action spectra may vary between species.

In particular, many of the flavonoids measured in my studies showed in the majority of the cases linear responsiveness to UV exclusion and could thus be predicted with the spectra tested. In contrast, chlorogenic acids showed strong non-linearity in their response to UV radiation in all experiments. This non-linearity of the dose responses offers an explanation why many of the concentrations of compounds and compound groups could not be predicted with the method used in my studies.

TABLE 2 Fit of expected relative responses for six different action spectra compared to relative responses of phenolic compounds in grey alder, white birch and silver birch. x = rejected at 5% risk level, • = not rejected. In the field experiment (III) there were four samplings during the growing season, in the outdoor experiment (IV) only one sampling at the end of the experiment. Summed phenolics in the outdoor experiment is with condensed tannins.

Phenolics	Sampling	GEN(G)	GEN(T)	CIE	FLAV	DNA(P)	PG
Grey alder (III)							
flavonoids (group)	all	x	x	•	•	•	x
quercetin 3-galactoside	all	x	x	x	x	•	•
kaempferol 3-glucoside	all	x	x	x	x	x	x
quercetin 3-glucoside	1	•	•	•	•	•	x
quercetin 3-arabinoside	1	•	•	•	•	•	•
"	2	•	•	•	•	•	x
White birch (III)							
flavonoids (group)	all	x	x	x	x	x	x
quercetin 3-galactoside	all	x	•	•	•	•	x
quercetin glycoside	all	x	•	•	•	•	•
kaempferol glucoside	all	•	•	•	•	•	•
quercetin 3-glucoside	1	x	x	x	x	x	•
"	2	•	•	•	•	•	•
"	3	•	•	•	•	x	x
"	4	•	•	•	•	•	•
Silver birch (IV)							
chlorogenic acid		x	x	x	x	x	x
flavonoids (group)		x	•	•	•	•	x
myricetin 3-galactoside		•	•	•	•	•	•
myricetin 3-rhamnoside		•	•	•	•	•	•
quercetin 3-galactoside		x	•	•	•	•	x
quercetin 3-rhamnoside		x	•	•	•	•	x
kaempferol 3-rhamnoside		x	•	•	•	•	x
condensed tannins (group)		•	•	•	•	•	•
summed phenolics		x	x	•	•	•	x

Taken together, of the three tree species and their varying composition of phenolic compounds and observed responses, GEN(G) and PG were the two spectra most consistently failing to predict the responses, GEN(T) matched with the observed responses slightly better and CIE, DNA(P) and FLAV were capable of predicting the observed responses well (Table 2). In other words, spectra with moderate effectiveness in both the UV-B and UV-A band were the ones best predicting the responses.

4.4 Enhancement errors in UV-B supplementation experiments

It has been thought that the differences in the UV-A region play a major role in determining the appropriateness of a BSWF when calculating the supplemental UV-flux from lamps used to simulate enhanced UV-B radiation in relation to stratospheric ozone depletion. As presented in my modeling study (V), this conclusion is derived from a situation where shading from lamp frames is compensated with radiation flux from the UV-lamps. This approach is not recommendable and can lead to large errors. Even if possibly resulting in lower absolute UV-B doses, having realistic irradiation schemes and importantly, a realistic treatment and control situation, favors the approach used in my assessment.

Past experiments simulating enhanced UV-B radiation in relation to stratospheric ozone depletion and measuring plant growth responses have most often used either CIE, GEN(G), GEN(T) or PG as a weighting function. My results suggest that most conclusions in such studies have simulated the target ozone depletion level well, no matter which one of the spectra has been used. In contrast, when shifting from growth responses to DNA damage, there is a possibility of a large distortion in the conclusions. This is because there is evidence that most of the variation in DNA damage density is caused by variations in the UV-B band. For such experiments DNA(N) has been demonstrated to be an appropriate spectrum (Rousseaux et al. 1999). According to the results of my study, if GEN(G) or CIE are used for calculating the UV-doses in such studies measuring DNA damage, the enhancement would be about two times more than the intended enhancement! Considering my results with phenolic metabolites and flavonoids in particular, CIE, DNA(P) and FLAV were capable of predicting the observed responses well. Consequently, if lamp burning times are set according to GEN(G) as a weighting function, the experiments would deliver from 0.6 to 1.1 times the intended enhancement.

Spectra with different effectiveness in the UV-A can yield very similar values of relative effectiveness for lamp radiation when compared to the effectiveness of increased solar UV radiation due to ozone depletion because it is the UV-B band where the effect is strongest. Following this, the action spectrum of the measured response in an experiment must be carefully determined, and when determining an appropriate BSWF, differences in the shape of action spectra in the whole UV-range from 290 to 400 nm have to be taken into consideration.

5 CONCLUSIONS

Both UV-A and UV-B radiation were found to affect leaf phenolic concentrations and other chemical properties of the three Betulaceae species, thus validating my first hypothesis. Additionally, changes in the concentration of all phenolic groups and changes in plant responses to UV radiation during a growing season in the two field experiments confirm my second hypothesis. Variation in the responses of phenolic metabolites to UV radiation emphasizes their multiple roles in plants. Consequently, future experiments concerning the effects of UV radiation on plant phenolics should examine individual phenolic compounds, rather than bulk concentrations. The effect of sampling time is also crucial. Furthermore, UV-induced changes in plant litter can affect decomposition processes by altering microbial communities and/or their activity in the soil, as illustrated by my third hypothesis.

Confirmation of my fourth hypothesis presents a challenge to experimental planning, as different BSWFs might be needed for individual phenolic metabolites and these may also be required to vary during a growing season. Careful choice of the BSWF best describing the responses of the organism or system under focus is very important, since it affects the interpretations of the results in relation to ozone depletion. The determination of an appropriate BSWF for an experiment supersedes my fifth hypothesis, since it requires careful assessment of the weight given by a weighting function not only to UV-A but to *both* the UV-A and UV-B bands. However, neither the experimental location nor cloudiness were important factors in defining the choice of an appropriate BSWF, so allowing me to reject my sixth hypothesis.

Conclusions drawn from past research with supplemental UV-B radiation concerning the effects of ozone depletion on DNA damage in plants and possibly also phenolics, call for retrospective analysis. The changes reported in this thesis in the chemistry of plant leaves and litter, and subsequent changes in soil respiration, make a strong case for the continuation of research into UV action spectra for different organisms. Consistency of approaches and development of new methodologies is essential to assess the effects of UV radiation on plants and other organisms with confidence. In addition, new

research should extend beyond ozone depletion, to focus on the role of UV radiation in terrestrial ecosystems as a source of information for plants and regulator of plant processes, and via plants to other trophic levels.

Acknowledgements

This study was carried out at the University of Jyväskylä, Department of Biological and Environmental Science. This project was financially supported by the Maj and Tor Nessling Foundation. In addition, I received funding for traveling from the Finnish Graduate School in Environmental Science and Technology (EnSTe) and from the Academy of Finland (decision no. 116775 to P.J. Aphalo).

I am most grateful to the best supervisors one can possibly have. Pedro J. Aphalo has the ability to offer his knowledge and guidance with endless patience, and he truly has not saved himself in guiding me during these years. Jari Haimi deserves big thanks for all his support and guidance, dating back already to my earlier studies and MSc thesis. I am grateful for his ability to encourage me through the not-so-encouraging moments, when the earthworms collected are of the wrong species and an experiment needs to be re-planned.

Although not officially, Riitta Tegelberg has really been my third supervisor. I have been privileged having her to share her insights and friendship with me.

I am thankful to Riitta Julkunen-Tiitto for being able to rely on her expertise on analysing plant secondary compounds and being able to work in her laboratories at the University of Joensuu.

Collaboration with Anders Lindfors and his colleagues at the Finnish Meteorological Institute provided excellent data and new perspectives to my thesis, without which this thesis would have been incomplete. The same applies to Bob O'Hara at the Department of Statistics, University of Helsinki, and his wizard-like ability to work out the statistics.

Sirkka Sutinen at the Finnish Forest Research Institute in Joensuu with her knowledge concerning measuring leaf anatomical features and Elina Vapaavuori at the Finnish Forest Research Institute in Suonenjoki with her expertise concerning leaf cell wall properties, ensured that I obtained essential data and a deeper insight into UV effects on plants.

I wish to thank everyone in the section of Environmental Science for all their support and advice. Practical phases of the experimental work in the laboratory required such expertise, that I would have been lost without Leena Siitonen in Jyväskylä and Sinikka Sorsa in Joensuu. Tuulia Venäläinen was responsible for successfully taking care of the outdoor experiment in year 2006 and doing the measurements and analyses involved. I would not have been able to analyse my numerous leaf samples and conduct the experiments without the help of Mustapha Bouchelham, Sari Vilhunen, Pasi Kemppainen, Anna Repo, Tanja Salakka, Kati Sivander, nor could I have managed without the help of all the technicians and administrative staff at the department. Emily Knott deserves thanks for checking the language of the summary.

Carlos Ballaré and colleagues at the Institute for Agricultural Plant Physiology and Ecology in the University of Buenos Aires deserve thanks for

their hospitality and inspiring discussions while I visited their laboratories in summer 2007.

Along the way, recent and former members of the “Soil Group” have offered guidance and peer support; memories of the little Christmas parties and wine tasting colloquiums are especially savoured. I would also like to thank Heikki Setälä, because he is the one who in the first place, back in year 1995, introduced me to the fascinating world of soil ecology; in the end is this thesis.

During the last year or so when writing this thesis I have been working at the section of Physiology and Neurosciences at the Department of Biosciences at the University of Helsinki: Kai Kaila, Eva Ruusuvuori, Juha Voipio and Katri Wegelius and colleagues are thanked for inspiring discussions. In addition, Kira Maisniemi, Luis Morales, Matthew Robson, Sari Siipola and Fang Wang from our SenPEP research group kindly provided that much needed peer support.

Late Elmeri was my faithful “field assistant”. While I collected my leaf samples, he chased voles and rabbits; those field trips are the essence of this thesis.

I thank all my friends and relatives for their love and support. I am grateful to my parents, who have always believed in me. And Vesa, I am the most fortunate one, for having you by my side.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Auringon UV-säteily ja kasvien vasteet: otsonikatoon liittyvien tutkimusten menetelmien arviointia

Ultraviolettisäteilyn (UV, 280-400 nm) ja erityisesti otsonikadon seurauksena lisääntyvän UV-B-säteilyn (280-320 nm) vaikutuksia kasveihin on tutkittu paljon parin viimeisen vuosikymmenen aikana. Säteilyltä suojaavan otsonikerroksen odotetaan palautuvan 1980-lukua edeltävälle tasolle arviolta vuoteen 2050 mennessä. Ilmastomuutokseen liittyvän hiilidioksidipitoisuuden nousun aiheuttaman yläilmakehän jäähtymisen vuoksi otsonikato arktisilla alueilla saattaa kuitenkin edelleen jatkua, vaikka otsonikatoa aiheuttavan kloorin ja bromin pitoisuus ilmakehässä laskisi. Ilmakehän hiilidioksidipitoisuuden kasvaessa alailmakehä lämpenee ja yläilmakehä jäähtyy, minkä seurauksena vapautuneet kloori- ja bromiatomit voivat toimia otsonia tuhoavien kemiallisten reaktioiden katalyytteinä.

UV-B-säteilyn mahdolliset haittavaikutukset liittyvät säteilyn nukleiinihapoille, proteiineille ja muille molekyyyleille aikaansaamiin vaurioihin. Osassa tutkimuksista on tämän seurauksena havaittu joitakin mm. kasvien kasvuun ja lehtien anatomiaan liittyviä vaikutuksia. Kasvit tuottavat fenolisia yhdisteitä, mm. flavonoideja, jotka suojaavat kasvisoluja säteilyltä. Fenoliset yhdisteet voivat vaikuttaa ekosysteemeihin laajemminkin, esimerkiksi orgaanisen aineksen hajotusprosessien kautta, ja on esitetty, että vaikka otsonikadon seurauksena lisääntyneen UV-B-säteilyn suorat vaikutukset olisivatkin vähäisiä, välilliset vaikutukset muiden trofiatasojen kautta voivat olla merkittäviä. Toistaiseksi näistä UV-säteilyn kokonaisvaikutuksista ekosysteemeihin tiedetään vielä vähän.

Otsonikadon seurauksena lisääntyvän UV-B-säteilyn vaikutuksia on tutkittu pääasiassa käyttämällä lamppuja lisäämään säteilyn määrää. Lamppujen tuottaman säteilyn ja otsonikadon seurauksena lisääntyvän säteilyn aallonpituudet ovat kuitenkin erilaiset. Kasvien vasteet puolestaan muuttuvat riippuen säteilyn aallonpituudesta (n.s. vaikutusspektri). Näitä vaikutusspektrejä käytetään painotuskertoimina laskettaessa vaadittavaa lamppujen päälläoloaikaa, joka puolestaan vastaa tavoitellun suuruisen otsonikadon aiheuttaman UV-B-säteilymäärän lisäystä.

Tämän työn tavoitteena oli tutkia UV-säteilyn vaikutuksia kolmen eri puulajin fenoliyhdisteiden tuotantoon käyttämällä kokeissa kalvoja, jotka poistavat säteilyn eri aallonpituusalueita. Tutkimuspuina käytettiin harmaaleppää (*Alnus incana*) ja hieskoivua (*Betula pubescens*) sekä rauduskoivun taimia (*Betula pendula*). Laboratoriossa tehdyissä hajotuskokeissa selvitettiin, välittyvätkö eri säteilyolosuhteiden aikaansaamat muutokset lehtien (karikkeen) kemiallisissa ominaisuuksissa kasvin kasvun aikana niiden hajoamisnopeuteen, maaperäeläimiin tai mikrobien hiilidioksidintuotantoon. Lisäksi tavoitteena oli kehittää uusia menetelmiä ja malleja otsonikatoon liittyvien tutkimusten tulosten arviointiin. Kokeissa verrattiin aikaisemmissa

tutkimuksissa käytettyjä painotuskertoimia, yhdistettynä mallinnettuun säteilymäärään ja käytettyjen kalvojen luomiin säteilyolosuhteisiin, mitattuihin kasvuvasteisiin. Lisäksi mallinnettiin aikaisempien kokeiden todellisesti simuloimaa otsonikadon määrää ja mahdollisia virheitä säteilymäärien lisäyksissä.

Tulokset osoittavat, että UV-säteilyn vaikutukset fenolisiin yhdisteisiin ovat vaihtelevia. Lisäksi muut tekijät vaikuttavat fenolisten yhdisteiden akkumulaation, sillä lähes kaikkien yhdisteiden pitoisuudet vaihtelivat kenttäkokeissa kasvukauden aikana, vaikka UV-säteilyllä ei kaikkiiin vaikutusta ollutkaan. UV-säteily aiheutti muutoksia myös hajotuskokeissa käytetyn karikkeen muihin kemiallisiin ominaisuuksiin, mm. hiilen ja ligniinin määriin. UV-säteilyn poistamisen aiheuttamien karikkeen kemiallisten muutosten seurauksena myös mikrobien hiilidioksidintuotanto muuttui. Karikkeen hajoamisnopeuteen ei käsittelyillä ollut vaikutusta. Tässä työssä saadut tulokset korostavat UV-säteilyn roolia ekosysteemeissä, ei pelkästään vaurioiden aiheuttajana, vaan kasvien informaatiolähteenä ja kasvun säätelijänä. Kasvien välityksellä UV-säteilyllä on merkittävät rooli myös hajotustoiminnassa ja ravinteiden kierrossa.

Otsonikatoon liittyvien tutkimusten ongelma on usein ollut se, että kasvien tuottamien fenolisten yhdisteiden määrää on tutkittu pääasiassa mittaamalla vain ns. kokonaisvastetta, eikä yksittäisten yhdisteiden akkumulaatiota. Yksittäisillä yhdisteillä on kuitenkin erilaisia tehtäviä kasveissa ja niiden vaikutukset esimerkiksi kasvinsyöjiin ja hajottajiin vaihtelevat, joten kokonaisvasteen mittaaminen ei riitä selvittämään lisääntyneen säteilyn kaikkia vaikutuksia. Myös näytteenottoajankohta voi vaikuttaa tutkimusten johtopäätöksiin.

Painotuskertoimien vertailu osoitti, että eri painotuskertoimia tarvitaan kasvien eri vasteita varten, eri kertoimia jopa yksittäisille fenolisille yhdisteille. Painotuskertoimen valintaan vaikuttavat sekä UV-B- että UV-A-alueen painotus. Mallinnustulosten perusteella voidaan sanoa, että otsonikadon vaikutusten ali- tai yliarviointi on suurempaa liittyen UV-säteilyn aiheuttamiin DNA-vaurioihin ja muutoksiin fenolisten yhdisteiden pitoisuuksissa kuin verrattuna kasvien kasvuvasteisiin, ja siksi DNA-vaurioita ja muutoksia ennustavien tutkimusten johtopäätöksiä tulisi tarkastella uudestaan. Kokonaisuudessaan kokeisiin, joissa lisätään UV-B-säteilyä lamppujen avulla liittyy paljon metodologisia ongelmia, joita olisi syytä tarkastella kriittisesti ja kehittää kokonaan uusia tutkimusmenetelmiä UV-säteilyn vaikutusten selvittämiseksi.

REFERENCES

- Aphalo, P. J., Vapaavuori, E., de la Rosa, T. M. & Lehto, T. 2009. Does supplemental UV-B radiation affect gas exchange and RuBisCO activity of *Betula pendula* seedlings grown in forest soil under greenhouse conditions? *Plant Ecol. Divers.* 2: 37-43.
- Appel, H. M. 1993. Phenolics in ecological interactions: The importance of oxidation. *J. Chem. Ecol.* 19: 1521-1552.
- Ballaré, C. L. 2009. Illuminated behaviour - phytochrome as a key regulator of light foraging and plant anti-herbivore defence. *Plant, Cell Environ.* 32: 713-725.
- Ballaré, C. L., Scopel, A. L., Stapleton, A. E. & Yanovsky, M. J. 1996. Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. *Plant Physiol.* 112: 161-170.
- Bardgett, R. D. 2005. *The Biology of Soil.* 242 p., Oxford University Press, Oxford.
- Bassman, J. H. 2004. Ecosystem consequences of enhanced solar ultraviolet radiation: Secondary plant metabolites as mediators of multiple trophic interactions in terrestrial plant communities. *Photochem. Photobiol.* 79: 382-398.
- Batschauer, A. 1998. Photoreceptors of higher plants. *Planta* 206: 479-492.
- Bilger, W., Rolland, M. & Nybakken, L. 2007. UV screening in higher plants induced by low temperature in the absence of UV-B radiation. *Photochem. Photobiol. Sci* 6: 190-195.
- Björn, L. O. 2007. Action spectroscopy in biology. In: Björn, L. O. (ed.), *Photobiology*: 139-154. Springer, New York.
- Boccalandro, H. E., Mazza, C. A., Mazzella, M. A., Casal, J. J. & Ballaré, C. L. 2001. Ultraviolet B radiation enhances a phytochrome-B-mediated photomorphogenic response in *Arabidopsis*. *Plant Physiol.* 126: 780-788.
- Bornman, J. F. 1999. Localisation and functional significance of flavonoids and related compounds. In: Rozema, J. (ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*: 59-69. Backhuys Publishers, Leiden, The Netherlands.
- Brosche, M. & Strid, Å. 2003. Molecular events following perception of ultraviolet-B radiation by plants. *Physiol. Plantarum* 117: 1-10.
- Brown, B. A. & Jenkins, G. I. 2008. UV-B signalling pathways with different fluence-rate response profiles are distinguished in mature *Arabidopsis* leaf tissue by requirement for UVR8, HY5 and HYH. *Plant Physiol.* 146: 576-588.
- Brown, B. A., Cloix, C., Jiang, G. H., Kaiserli, E., Herzyk, P., Kliebenstein, D. J. & Jenkins, G. I. 2005. A UV-B-specific signaling component orchestrates plant UV protection. *PNAS* 102: 18225-18230.

- Caldwell, M. M. 1971. Solar ultraviolet radiation and the growth and development of higher plants. In: Giese, A. C. (ed.), *Photophysiology*: 131-177. Academic Press, New York.
- Caldwell, M. M. & Flint, S. D. 1997. Uses of biological spectral weighting functions and the need of scaling for the ozone reduction problem. *Plant Ecol.* 128: 67-76.
- Caldwell, M. M., Bornman, J. F., Ballaré, C. L., Flint, S. D. & Kulandaivelu, G. 2007. Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. *Photochem. Photobiol. Sci.* 6: 252-266.
- Casal, J. J. 2000. Phytochromes, cryptochromes, phototropin: Photoreceptor interactions in plants. *Photochem. Photobiol.* 71: 1-11.
- Chen, M., Chory, J. & Fankhauser, C. 2004. Light signal transduction in higher plants. *Annu. Rev. Genet.* 38: 87-117.
- Convey, P., Pugh, P. J. A., Jackson, C., Murray, A. W., Ruhland, C. T., Xiong, F. S. & Day, T. A. 2002. Response of antarctic terrestrial microarthropods to long-term climate manipulations. *Ecology* 83: 3130-3140.
- Day, T. A. & Neale, P. J. 2002. Effects of UV-B radiation on terrestrial and aquatic primary producers. *Ann. Rev. Ecol. Syst.* 33: 371-396.
- Farman, J. C., Gardiner, B. G. & Shanklin, J. D. 1985. Large losses of total ozone in antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* 315: 207-210.
- Flint, S. D. & Caldwell, M. M. 2003a. A biological spectral weighting function for ozone depletion research with higher plants. *Physiol. Plantarum* 117: 137-144.
- Flint, S. D. & Caldwell, M. M. 2003b. Field testing of UV biological spectral weighting functions for higher plants. *Physiol. Plantarum* 117: 145-153.
- Flint, S. D., Ryel, R. J. & Caldwell, M. M. 2003. Ecosystem UV-B experiments in terrestrial communities: A review of recent findings and methodologies. *Agr. Forest Meteorol.* 120: 177-189.
- Flint, S. D., Searles, P. S. & Caldwell, M. M. 2004. Field testing of biological spectral weighting functions for induction of UV-absorbing compounds in higher plants. *Photochem. Photobiol.* 79: 399-403.
- von der Gathen, P., Rex, M., Harris, N. R. P., Lucic, D., Knudsen, B. M., Braathen, G. O., De Backer, H., Fabian, R., Fast, H., Gil, M., Kyrö, E., Mikkelsen, I. S., Rummukainen, M., Stahelin, J. & Varotsos, C. 1995. Observational evidence for chemical ozone depletion over the arctic in winter 1991-92. *Nature* 375: 131-134.
- Ghetti, F., Bagnoli, C. & Checcucci, G. 2006. Response to UV-B radiation: Weighting functions and action spectra. In: Ghetti, F., Checcucci, G. & Bornman, J. F. (eds), *Environmental UV Radiation: Impact on Ecosystems and Human Health and Predictive Models*: 85-93. Springer, The Netherlands.

- Green, A. E. S., Sawada, T. & Shettle, E. P. 1974. The middle ultraviolet reaching the ground. *Photochem. Photobiol.* 19: 251-259.
- Hagerman, A. E. 1995. *Tannin Chemistry*. 66 p., Department of Chemistry, Miami University, Miami.
- Haukioja, E. 2005. Plant defenses and population fluctuations of forest defoliators: Mechanism-based scenarios. *Ann. Zool. Fennici* 42: 313-325.
- Hegglin, M. I. & Shepherd, T. G. 2009. Large climate-induced changes in ultraviolet index and stratosphere-to-troposphere ozone flux. *Nature Geosci.* 2: 687-691.
- van der Heijden, M. G. A., Bardgett, R. D. & van Straalen, N. M. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11: 296-310.
- Ibdah, M., Krins, A., Seidlitz, H. K., Heller, W., Strack, D. & Vogt, T. 2002. Spectral dependence of flavonol and betacyanin accumulation in *Mesembryanthemum crystallinum* under enhanced ultraviolet radiation. *Plant, Cell Environ.* 25: 1145-1154.
- Jansen, M. A. K., Gaba, V. & Greenberg, B. M. 1998. Higher plants and UV-B radiation: Balancing damage, repair and acclimation. *Trends Plant Sci* 3: 131-135.
- Jenkins, G. I., Long, J. C., Wade, H. K., Shenton, M. R. & Bibikova, T. N. 2001. UV and blue light signalling: Pathways regulating chalcone synthase gene expression in *Arabidopsis*. *New Phytol.* 151: 121-131.
- Jiao, Y., Lau, O. S. & Deng, X. W. 2007. Light-regulated transcriptional networks in higher plants. *Nat. Rev. Genet.* 8: 217-230.
- Johnson, D., Campbell, C. D., Lee, J. A., Callaghan, T. V. & Gwynn-Jones, D. 2002. Arctic microorganisms respond more to elevated UV-B radiation than CO₂. *Nature* 416: 82-83.
- Jones, C. G. & Hartley, S. E. 1999. A protein competition model of phenolic allocation. *Oikos* 86: 27-44.
- Jones, L. W. & Kok, B. 1966. Photoinhibition of chloroplast reactions. II. multiple effects. *Plant Physiol.* 41: 1044-1049.
- Julkunen-Tiitto, R., Häggman, H., Aphalo, P. J., Lavola, A., Tegelberg, R. & Veteli, T. 2005. Growth and defense in deciduous trees and shrubs under UV-B. *Environ. Pollut.* 137: 404-414.
- Keiller, D. R. & Holmes, M. G. 2001. Effects of long-term exposure to elevated UV-B radiation on the photosynthetic performance of five broad-leaved tree species. *Photosynthesis Res.* 67: 229-240.
- Keinänen, M. & Julkunen-Tiitto, R. 1998. High-performance liquid chromatographic determination of flavonoids in *Betula pendula* and *Betula pubescens* leaves. *J. Chromatogr. A* 793: 370-377.
- Keski-Saari, S., Pusenius, J. & Julkunen-Tiitto, R. 2005. Phenolic compounds in seedlings of *Betula pubescens* and *B. pendula* are affected by enhanced UV-B radiation and different nitrogen regimens during early ontogeny. *Global Change Biol.* 11: 1180-1194.

- Kinnunen, H., Huttunen, S. & Laakso, K. 2001. UV-absorbing compounds and waxes of scots pine needles during a third growing season of supplemental UV-B. *Environ. Pollut.* 112: 215-220.
- Kivimäenpää, M., Jönsson, A. M., Stjernquist, I., Selldén, G. & Sutinen, S. 2004. The use of light and electron microscopy to assess the impact of ozone on norway spruce needles. *Environ. Pollut.* 127: 441-453.
- Kolb, C. A. & Pfündel, E. E. 2005. Origins of non-linear and dissimilar relationships between epidermal UV absorbance and UV absorbance of extracted phenolics in leaves of grapevine and barley. *Plant, Cell Environ.* 28: 580-590.
- Kostina, E., Wulff, A. & Julkunen-Tiitto, R. 2001. Growth, structure, stomatal responses and secondary metabolites of birch seedlings (*Betula pendula*) under elevated UV-B radiation in the field. *Trees* 15: 483-491.
- Kraus, T. E. C., Dahlgren, R. A. & Zasoski, R. J. 2003. Tannins in nutrient dynamics of forest ecosystems - a review. *Plant Soil* 256: 41-66.
- Laitinen, M., Julkunen-Tiitto, R. & Rousi, M. 2002. Foliar phenolic composition of european white birch during bud unfolding and leaf development. *Physiol. Plantarum* 114: 450-460.
- Landry, L. G., Chapple, C. C. S. & Last, R. L. 1995. Arabidopsis mutants lacking phenolic sunscreens exhibit enhanced ultraviolet-B injury and oxidative damage. *Plant Physiol.* 109: 1159-1166.
- Lavola, A. 1998a. Accumulation of flavonoids and related compounds in birch induced by UV-B irradiance. *Tree Physiol.* 18: 53-58.
- Lavola, A. 1998b. Phytochemicals of deciduous trees in relation to environmental changes. PhD thesis, University of Joensuu, Publications in Science 46, 7-39.
- Lavola, A., Julkunen-Tiitto, R., Aphalo, P. J., de la Rosa, T. M. & Lehto, T. 1997. The effect of UV-B radiation on UV-absorbing secondary metabolites in birch seedlings grown under simulated forest soil conditions. *New Phytol.* 137: 617-621.
- Li, J., Ou-Lee, T. M., Raba, R., Amundson, R. G. & Last, R. L. 1993. Arabidopsis flavonoid mutants are hypersensitive to UV-B irradiation. *Plant Cell* 5: 171-179.
- Li, F., Stolarski, R. S. & Newman, P. A. 2009. Stratospheric ozone in the post-CFC era. *Atmos. Chem. Phys.* 9: 2207-2213.
- Liakoura, V., Manetas, Y. & Karabourniotis, G. 2001. Seasonal fluctuations in the concentration of UV-absorbing compounds in the leaves of some mediterranean plants under field conditions. *Physiol. Plantarum* 111: 491-500.
- Lindfors, A., Heikkilä, A., Kaurola, J., Koskela, T. & Lakkala, K. 2009. Reconstruction of solar spectral surface UV irradiances using radiative transfer simulations. *Photochem. Photobiol.* 85: 1233-1239.
- Madronich, S., McKenzie, R. L., Björn, L. O. & Caldwell, M. M. 1998. Changes in biologically active ultraviolet radiation reaching the earth's surface. *J. Photochem. Photobiol. B* 46: 5-19.

- Martz, F., Sutinen, M., Derome, K., Wingsle, G., Julkunen-Tiitto, R. & Turunen, M. 2007. Effects of ultraviolet (UV) exclusion on the seasonal concentration of photosynthetic and UV-screening pigments in scots pine needles. *Global Change Biol.* 13: 252-265.
- Mazza, C. A., Bocalandro, H. E., Giordano, C. V., Battista, D., Scopel, A. L. & Ballaré, C. L. 2000. Functional significance and induction by solar radiation of ultraviolet-absorbing sunscreens in field-grown soybean crops. *Plant Physiol.* 122: 117-126.
- McDonald, M. S. 2003. Light and pigments. In: McDonald, M. S. (ed.), *Photobiology of Higher Plants*: 1-32. Wiley, England.
- McKenzie, R. L., Aucamp, P. J., Bais, A. F., Björn, L. O. & Ilyas, M. 2007. Changes in biologically-active ultraviolet radiation reaching the Earth's surface. *Photochem. Photobiol. Sci.* 6: 218-231.
- McKinlay, A. F. & Diffey, B. L. 1987. A reference action spectrum for ultra-violet induced erythema in human skin. In: Passchier, W. F. & Bosnjakovic, B. F. M. (eds), *Human Exposure to Ultraviolet Radiation: Risks and Regulations*: 83-87. Elsevier, Amsterdam.
- McLandress, C. & Shepherd, T. G. 2009. Simulated anthropogenic changes in the brewer-dobson circulation, including its extension to high latitudes. *J. Clim.* 22: 1516-1540.
- Musil, C. F. 1995. Differential effects of elevated ultraviolet-B radiation on the photochemical and reproductive performances of dicotyledonous and monocotyledonous arid-environment ephemerals. *Plant, Cell Environ.* 18: 844-854.
- Nagel, L. M., Bassman, J. H., Edwards, G. E., Robberecht, R. & Franceschi, V. R. 1998. Leaf anatomical changes in *Populus trichocarpa*, *Quercus rubra*, *Pseudotsuga menziesii* and *Pinus ponderosa* exposed to enhanced ultraviolet-B radiation. *Physiol. Plantarum* 104: 385-396.
- O'Connor, F. B. 1962. The extraction of enchytraeidae from soil. In: Murphy, P. W. (ed.), *Progress in Soil Zoology*: 279-285. Butterworths, London.
- Olsen, K. M., Slimestad, R., Lea, U. S., Brede, C., Løwdal, T., Ruoff, P., Verheul, M. & Lillo, C. 2009. Temperature and nitrogen effects on regulators and products of the flavonoid pathway: Experimental and kinetic model studies. *Plant, Cell Environ.* 32: 286-299.
- Ossipov, V., Loponen, J., Ossipova, S., Haukioja, E. & Pihlaja, K. 1997. Gallotannins of birch *Betula pubescens* leaves: HPLC separation and quantification. *Biochem Syst Ecol* 25: 493-504.
- Pancotto, V. A., Sala, O. E., Cabello, M., Lopez, N. I., Robson, T. M., Ballaré, C. L., Caldwell, M. M. & Scopel, A. L. 2003. Solar UV-B decreases decomposition in herbaceous plant litter in tierra del fuego, argentina: Potential role of an altered decomposer community. *Global Change Biol.* 9: 1465-1474.
- Pancotto, V. A., Sala, O. E., Robson, T. M., Caldwell, M. M. & Scopel, A. L. 2005. Direct and indirect effects of solar ultraviolet-B radiation on long-term decomposition. *Global Change Biol.* 11: 1982-1989.

- Paul, N., Callaghan, T., Moody, S., Gwynn-Jones, D. & Gehrke, C. 1999. UV-B impacts on decomposition biochemical cycling. In: Rozema, J. (ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*: 117-133. Backhuys Publishers, Leiden, The Netherlands.
- Paul, N. D. & Gwynn-Jones, D. 2003. Ecological roles of solar UV radiation: Towards an integrated approach. *Trends Ecol. Evol.* 18: 48-55.
- Paul, N. D., Rasanayagam, S., Moody, S. A., Hatcher, P. E. & Ayres, P. G. 1997. The role of interactions between trophic levels in determining the effects of UV-B on terrestrial ecosystems. *Plant Ecol.* 128: 297-308.
- Pinheiro, J. C. & Bates, D.M. 2000. *Mixed-Effects Models in S and S-Plus*. 528 p., Springer, New York.
- Porra, R. J., Thompson, W. A. & Kriedemann, P. E. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: Verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochim Biophys Acta* 975: 384-394.
- Quate, F. E., Sutherland, B. M. & Sutherland, J. C. 1992. Action spectrum for DNA damage in alfalfa lowers predicted impact of ozone depletion. *Nature* 358: 576-578.
- R Development Core Team. 2006. *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.
- Raich, J. W. & Tufekcioglu, A. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* 48: 70-90.
- Raich, J. W., Potter, C. S. & Bhagawati, D. 2002. Interannual variability in global soil respiration, 1980-94. *Global Change Biol.* 8: 800-812.
- Riipi, M., Ossipov, V., Lempa, K., Haukioja, E., Koricheva, J., Ossipova, S. & Pihlaja, K. 2002. Seasonal changes in birch leaf chemistry: Are there trade-offs between leaf growth and accumulation of phenolics? *Oecologia* 130: 380-390.
- Rinnan, R., Keinänen, M. M., Kasurinen, A., Asikainen, J., Kekki, T. K., Holopainen, T., Ro-Poulsen, H., Mikkelsen, T. N. & Michelsen, A. 2005. Ambient ultraviolet radiation in the arctic reduces root biomass and alters microbial community composition but has no effects on microbial biomass. *Global Change Biol.* 11: 564-574.
- Robson, T. M., Pancotto, V. A., Scopel, A. L., Flint, S. D. & Caldwell, M. M. 2005. Solar UV-B influences microfaunal community composition in a tierra del fuego peatland. *Soil Biol. Biochem.* 37: 2205-2215.
- de la Rosa, T. M., Julkunen-Tiitto, R., Lehto, T. & Aphalo, P. J. 2001. Secondary metabolites and nutrient concentrations in silver birch seedlings under five levels of daily UV-B exposure and two relative nutrient addition rates. *New Phytol.* 150: 121-131.
- de la Rosa, T. M., Aphalo, P. J. & Lehto, T. 2003. Effects of ultraviolet-B radiation on growth, mycorrhizas and mineral nutrition of silver birch (*Betula*

- pendula Roth) seedlings grown in low-nutrient conditions. *Global Change Biol.* 9: 65-73.
- Rousseaux, M. C., Ballaré, C. L., Giordano, C. V., Scopel, A. L., Zima, A. M., Szwarcberg-Bracchitta, M., Searles, P. S., Caldwell, M. M. & Díaz, S. B. 1999. Ozone depletion and UVB radiation: Impact on plant DNA damage in southern south america. *PNAS* 96: 15310-15315.
- Rozema, J., van de Staaij, J., Björn, L.O. & De Baker, N. 1999. Depletion of stratospheric ozone and solar UV-B radiation: Evolution of land plants, UV-screens and functions of polyphenolics. In: Rozema, J. (ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*: 1-19. Backhuys Publishers, Leiden, The Netherlands.
- Rozema, J., Boelen, P. & Blokker, P. 2005. Depletion of stratospheric ozone over the antarctic and arctic: Responses of plants of polar terrestrial ecosystems to enhanced UV-B, an overview. *Environ Pollut* 137: 428-442.
- Salminen, J., Ossipov, V., Haukioja, E. & Pihlaja, K. 2001. Seasonal variation in the content of hydrolysable tannins in leaves of *Betula pubescens*. *Phytochemistry* 57: 15-22.
- 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.
- Setlow, R. B. 1974. The wavelengths in sunlight effective in producing skin cancer: A theoretical analysis. *PNAS* 71: 3363-3366.
- Shindell, D. T., Rind, D. & Lonergan, P. 1998. Increased polar stratospheric ozone losses and delayed eventual recovery owing to increasing greenhouse-gas concentrations. *Nature* 392: 589-592.
- Sohlenius, B. 1979. A carbon budget for nematodes, rotifers and tardigrades in a swedish coniferous forest soil. *Holarctic Ecol.* 2: 30-40.
- Suesslin, C. & Frohnmeyer, H. 2003. An *Arabidopsis* mutant defective in UV-B light-mediated responses. *Plant J.* 33: 591-601.
- Sullivan, J. H., Gitz III, D. C., Liu-Gitz, L., Xu, C., Gao, W. & Slusser, J. 2007. Coupling short-term changes in ambient UV-B levels with induction of UV-screening compounds. *Photochem. Photobiol.* 83: 863-870.
- Suomela, J., Ossipov, V. & Haukioja E. 1995. Variation among and within mountain birch trees in foliage phenols, carbohydrates and amino acids, and in growth of *Epirrita autumnata* larvae. *J. Chem. Ecol.* 21: 1421-1446.
- Taalas, P., Kaurola, J., Kylling, A., Shindell, D. T., Sausen, R., Dameris, M., Grewe, W., Herman, J., Damski, J. & Steil, B. 2000. The impact of greenhouse gases and halogenated species on the future solar UV radiation doses. *Geophys. Res. Lett.* 27: 1127-1130.
- Tegelberg, R. 2002. Impact of elevated ultraviolet-B radiation on three northern deciduous woody plants. University of Joensuu, PhD Dissertations in Biology 11, 7-31.
- Tegelberg, R., Julkunen-Tiitto, R. & Aphalo, P. J. 2001. The effects of long-term elevated UV-B on the growth and phenolics of field-grown silver birch (*Betula pendula*). *Global Change Biol.* 7: 839-848.

- Thimijan, R. W., Carns, H. R. & Campbell, L. E. 1978. Final Report (EPA-IAG-D6-0168): Radiation sources and related environmental control for biological and climatic effects UV research (BACER). Environmental Protection Agency, Washington, DC.
- Turunen, M., Heller, W., Stich, S., Sandermann, H., Sutinen, M. & Norokorpi, Y. 1999. The effects of UV exclusion on the soluble phenolics of young scots pine seedlings in the subarctic. *Environ. Pollut.* 106: 219-228.
- Ulm, R. & Nagy, F. 2005. Signalling and gene regulation in response to ultraviolet light. *Curr. Opin. Plant Biol.* 8: 477-482.
- Vogelmann, T. C. 1993. Plant tissue optics. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 44: 231.
- Waterman, P. G. & Mole, S. 1994. Analysis of phenolic plant metabolites. 238 p., Blackwell Scientific Publications, Oxford.
- Zepp, R. G., Erickson III, D. J., Paul, N. D. & Sulzberger, B. 2007. Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochem. Photobiol. Sci.* 6: 286-300.
- Zimmer, M. & Topp, W. 2000. Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). *J. Anim. Ecol.* 69: 1071-1082.

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 1 RAATIKAINEN, M. & VASARAINEN, A., Damage caused by timothy flies (*Amaurosome* spp.) in Finland, pp. 3-8.
SÄRKKÄ, J., The numbers of *Tubifex tubifex* and its cocoons in relation to the mesh size, pp. 9-13.
ELORANTA, P. & ELORANTA, A., Keuruselän kalastosta ja sen rakenteesta. - On the fish fauna of Lake Keuruselkä, Finnish Lake District, pp. 14-29.
ELORANTA, P. & ELORANTA, A., Kuusveden veden laadusta, kasviplanktonista ja kalastosta. - On the properties of water, phytoplankton and fish fauna of Lake Kuusvesi, Central Finland, pp. 30-47. 47 p. 1975.
- 2 ELORANTA, V., Effects of different process wastes and main sewer effluents from pulp mills on the growth and production of *Ankistrodesmus falcatus* var. *acicularis* (Chlorophyta), pp. 3-33.
ELORANTA, P. & KUNNAS, S., A comparison of littoral periphyton in some lakes of Central Finland, pp. 34-50.
ELORANTA, P., Phytoplankton and primary production in situ in the lakes Jyväsjärvi and North Päijänne in summer 1974, pp. 51-66. 66 p. 1976.
- 3 RAATIKAINEN, M., HALKKA, O., VASARAINEN, A. & HALKKA, L., Abundance of *Philaenus spumarius* in relation to types of plant community in the Tvärminne archipelago, southern Finland. 38 p. 1977
- 4 HAKKARI, L., On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. 87 p. 1978.
- 5 KÄPYLÄ, M., Bionomics of five woodnesting solitary species of bees (Hym., Megachilidae), with emphasis on flower relationships. 89 p. 1978.
- 6 KANKAALA, P. & SAARI, V., The vascular flora of the Vaarunvuoret hills and its conservation, pp. 3-62.
TÖRMÄLÄ, T. & KOVANEN, J., Growth and ageing of magpie (*Pica pica* L.) nestlings, pp. 63-77. 77 p. 1979.
- 7 VIITALA, J., Hair growth patterns in the vole *Clethrionomys rufocanus* (Sund.), pp. 3-17.
NIEMI, R. & HUHTA, V., Oribatid communities in artificial soil made of sewage sludge and crushed bark, pp. 18-30. 30 p. 1981.
- 8 TÖRMÄLÄ, T., Structure and dynamics of reserved field ecosystem in central Finland. 58 p. 1981.
- 9 ELORANTA, V. & KUIVASNIEMI, K., Acute toxicity of two herbicides, glyphosate and 2,4-D, to *Selenastrum capricornutum* Printz (Chlorophyta), pp. 3-18.
ELORANTA, P. & KUNNAS, S., Periphyton accumulation and diatom communities on artificial substrates in recipients of pulp mill effluents, pp. 19-33.
ELORANTA, P. & MARJA-AHO, J., Transect studies on the aquatic macrophyte vegetation of Lake Saimaa in 1980, pp. 35-65. 65 p. 1982.
- 10 LAKE PÄIJÄNNE SYMPOSIUM. 199 p. 1987.
- 11 SAARI, V. & OHENOJA, E., A check-list of the larger fungi of Central Finland. 74 p. 1988.
- 12 KOJOLA, I., Maternal investment in semi-domesticated reindeer (*Rangifer t. tarandus* L.). 26 p. Yhteenveto 2 p. 1989.
- 13 MERILÄINEN, J. J., Impact of an acid, polyhumic river on estuarine zoobenthos and vegetation in the Baltic Sea, Finland. 48 p. Yhteenveto 2 p. 1989.
- 14 LUMME, I., On the clone selection, ectomy-corrhizal inoculation of short-rotation willows (*Salix* spp.) and on the effects of some nutrients sources on soil properties and plant nutrition. 55 p. Yhteenveto 3 p. 1989.
- 15 KUITUNEN, M., Food, space and time constraints on reproduction in the common treecreeper (*Certhia familiaris* L.) 22 p. Yhteenveto 2 p. 1989.
- 16 YLÖNEN, H., Temporal variation of behavioural and demographical processes in cyclic *Clethrionomys* populations. 35 p. Yhteenveto 2 p. 1989.
- 17 MIKKONEN, A., Occurrence and properties of proteolytic enzymes in germinating legume seeds. 61 p. Yhteenveto 1 p. 1990.
- 18 KAINULAINEN, H., Effects of chronic exercise and ageing on regional energy metabolism in heart muscle. 76 p. Yhteenveto 1 p. 1990.
- 19 LAKSO, MERJA, Sex-specific mouse testosterone 16 α -hydroxylase (cytochrome P450) genes: characterization and genetic and hormonal regulations. 70 p. Yhteenveto 1 p. 1990.
- 20 SETÄLÄ, HEIKKI, Effects of soil fauna on decomposition and nutrient dynamics in coniferous forest soil. 56 p. Yhteenveto 2 p. 1990.
- 21 NÄRVÄNEN, ALE, Synthetic peptides as probes for protein interactions and as antigenic epitopes. 90 p. Yhteenveto 2 p. 1990.
- 22 ECOTOXICOLOGY SEMINAR, 115 p. 1991.
- 23 ROSSI, ESKO, An index method for environmental risk assessment in wood processing industry. 117 p. Yhteenveto 2 p. 1991.
- 24 SUHONEN, JUUKA, Predation risk and competition in mixed species tit flocks. 29 p. Yhteenveto 2 p. 1991.
- 25 SUOMEN MUUTTUVUUS LUONTO. Mikko Raatikaiselle omistettu juhla-kirja. 185 p. 1992.
- 26 KOSKIVAARA, MARI, Monogeneans and other parasites on the gills of roach (*Rutilus rutilus*) in Central Finland. Differences between four lakes and the nature of dactylogyrid communities. 30 p. Yhteenveto 2 p. 1992.
- 27 TASKINEN, JOUNI, On the ecology of two Rhipidocotyle species (Digenea: Bucephalidae) from two Finnish lakes. 31 p. Yhteenveto 2 p. 1992.
- 28 HUOVILA, ARI, Assembly of hepatitis B surface antigen. 73 p. Yhteenveto 1 p. 1992.
- 29 SALONEN, VEIKKO, Plant colonization of harvested peat surfaces. 29 p. Yhteenveto 2 p. 1992.

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 30 JOKINEN, ILMARI, Immunoglobulin production by cultured lymphocytes of patients with rheumatoid arthritis: association with disease severity. 78 p. Yhteenveto 2 p. 1992.
- 31 PUNNONEN, Eeva-Liisa, Ultrastructural studies on cellular autophagy. Structure of limiting membranes and route of enzyme delivery. 77 p. Yhteenveto 2 p. 1993.
- 32 HAIMI, JARI, Effects of earthworms on soil processes in coniferous forest soil. 35 p. Yhteenveto 2 p. 1993.
- 33 ZHAO, GUOCHANG, Ultraviolet radiation induced oxidative stress in cultured human skin fibroblasts and antioxidant protection. 86 p. Yhteenveto 1 p. 1993.
- 34 RÄTTI, OSMO, Polyterritorial polygyny in the pied flycatcher. 31 p. Yhteenveto 2 p. 1993.
- 35 MARJOMÄKI, VARPU, Endosomes and lysosomes in cardiomyocytes. A study on morphology and function. 64 p. Yhteenveto 1 p. 1993.
- 36 KIHILSTRÖM, MARKKU, Myocardial antioxidant enzyme systems in physical exercise and tissue damage. 99 p. Yhteenveto 2 p. 1994.
- 37 MUOTKA, TIMO, Patterns in northern stream guilds and communities. 24 p. Yhteenveto 2 p. 1994.
- 38 EFFECT OF FERTILIZATION ON FOREST ECOSYSTEM 218 p. 1994.
- 39 KERVINEN, JUKKA, Occurrence, catalytic properties, intracellular localization and structure of barley aspartic proteinase. 65 p. Yhteenveto 1 p. 1994.
- 40 MAPPES, JOHANNA, Maternal care and reproductive tactics in shield bugs. 30 p. Yhteenveto 3 p. 1994.
- 41 SIIKAMÄKI, PIIRKKO, Determinants of clutch-size and reproductive success in the pied flycatcher. 35 p. Yhteenveto 2 p. 1995.
- 42 MAPPES, TAPIO, Breeding tactics and reproductive success in the bank vole. 28 p. Yhteenveto 3 p. 1995.
- 43 LAITINEN, MARKKU, Biomonitoring of the responses of fish to environmental stress. 39 p. Yhteenveto 2 p. 1995.
- 44 LAPPALAINEN, PEKKA, The dinuclear Cu centre of cytochrome oxidase. 52 p. Yhteenveto 1 p. 1995.
- 45 RINTAMÄKI, PEKKA, Male mating success and female choice in the lekking black grouse. 23 p. Yhteenveto 2 p. 1995.
- 46 SUURONEN, TIINA, The relationship of oxidative and glycolytic capacity of longissimus dorsi muscle to meat quality when different pig breeds and crossbreeds are compared. 112 p. Yhteenveto 2 p. 1995.
- 47 KOSKENNIEMI, ESA, The ecological succession and characteristics in small Finnish polyhumic reservoirs. 36 p. Yhteenveto 1 p. 1995.
- 48 HOVI, MATTI, The lek mating system in the black grouse: the role of sexual selection. 30 p. Yhteenveto 1 p. 1995.
- 49 MARTTILA, SALLA, Differential expression of aspartic and cyteine proteinases, glutamine synthetase, and a stress protein, HVA1, in germinating barley. 54 p. Yhteenveto 1 p. 1996.
- 50 HUHTA, ESA, Effects of forest fragmentation on reproductive success of birds in boreal forests. 26 p. Yhteenveto 2 p. 1996.
- 51 OJALA, JOHANNA, Muscle cell differentiation in vitro and effects of antisense oligodeoxyribonucleotides on gene expression of contractile proteins. 157 p. Yhteenveto 2 p. 1996.
- 52 PALOMÄKI, RISTO, Biomass and diversity of macrozoobenthos in the lake littoral in relation to environmental characteristics. 27 p. Yhteenveto 2 p. 1996.
- 53 PUSENIUS, JYRKI, Intraspecific interactions, space use and reproductive success in the field vole. 28 p. Yhteenveto 2 p. 1996.
- 54 SALMINEN, JANNE, Effects of harmful chemicals on soil animal communities and decomposition. 28 p. Yhteenveto 2 p. 1996.
- 55 KOTIAHO, JANNE, Sexual selection and costs of sexual signalling in a wolf spider. 25 p. (96 p.). Yhteenveto 2 p. 1997.
- 56 KOSKELA, JUHA, Feed intake and growth variability in Salmonids. 27p. (108 p.). Yhteenveto 2 p. 1997.
- 57 NAARALA, JONNE, Studies in the mechanisms of lead neurotoxicity and oxidative stress in human neuroblastoma cells. 68 p. (126 p.). Yhteenveto 1 p. 1997.
- 58 AHO, TEIJA, Determinants of breeding performance of the Eurasian treecreeper. 27 p. (130 p.). Yhteenveto 2 p. 1997.
- 59 HAAPARANTA, AHTI, Cell and tissue changes in perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in relation to water quality. 43 p. (112 p.). Yhteenveto 3 p. 1997.
- 60 SOIMASUO, MARKUS, The effects of pulp and paper mill effluents on fish: a biomarker approach. 59 p. (158 p.). Yhteenveto 2 p. 1997.
- 61 MIKOLA, JUHA, Trophic-level dynamics in microbial-based soil food webs. 31 p. (110 p.). Yhteenveto 1 p. 1997.
- 62 RAHKONEN, RIITTA, Interactions between a gull tapeworm *Diphyllobothrium dendriticum* (Cestoda) and trout (*Salmo trutta* L.). 43 p. (69 p.). Yhteenveto 3 p. 1998.
- 63 KOSKELA, ESA, Reproductive trade-offs in the bank vole. 29 p. (94 p.). Yhteenveto 2 p. 1998.
- 64 HORNE, TAINA, Evolution of female choice in the bank vole. 22 p. (78 p.). Yhteenveto 2 p. 1998.
- 65 PIRHONEN, JUHANI, Some effects of cultivation on the smolting of two forms of brown trout (*Salmo trutta*). 37 p. (97 p.). Yhteenveto 2 p. 1998.
- 66 LAAKSO, JOUNI, Sensitivity of ecosystem functioning to changes in the structure of soil food webs. 28 p. (151 p.). Yhteenveto 1 p. 1998.
- 67 NIKULA, TUOMO, Development of radiolabeled monoclonal antibody constructs: capable of transporting high radiation dose into cancer cells. 45 p. (109 p.). Yhteenveto 1 p. 1998.

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 68 AIRENNE, KARI, Production of recombinant avidins in *Escherichia coli* and insect cells. 96 p. (136 p.). Yhteenveto 2 p. 1998.
- 69 LYYTIKÄINEN, TAPANI, Thermal biology of underyearling Lake Inari Arctic Charr *Salvelinus alpinus*. 34 p. (92 p.). Yhteenveto 1 p. 1998.
- 70 VIHINEN-RANTA, MAIJA, Canine parvovirus. Endocytic entry and nuclear import. 74 p. (96 p.). Yhteenveto 1 p. 1998.
- 71 MARTIKAINEN, ESKO, Environmental factors influencing effects of chemicals on soil animals. Studies at population and community levels. 44 p. (137 p.). Yhteenveto 1 p. 1998.
- 72 AHLROTH, PETRI, Dispersal and life-history differences between waterstrider (*Aquarius najas*) populations. 36 p. (98 p.). Yhteenveto 1 p. 1999.
- 73 SIPPONEN, MATTI, The Finnish inland fisheries system. The outcomes of private ownership of fishing rights and of changes in administrative practices. 81 p. (188 p.). Yhteenveto 2 p. 1999.
- 74 LAMMI, ANTTI, Reproductive success, local adaptation and genetic diversity in small plant populations. 36 p. (107 p.). Yhteenveto 4 p. 1999.
- 75 NIVA, TEUVO, Ecology of stocked brown trout in boreal lakes. 26 p. (102 p.). Yhteenveto 1 p. 1999.
- 76 PULKKINEN, KATIJA, Transmission of *Triaenophorus crassus* from copepod first to coregonid second intermediate hosts and effects on intermediate hosts. 45 p. (123 p.). Yhteenveto 3 p. 1999.
- 77 PARRI, SILJA, Female choice for male drumming characteristics in the wolf spider *Hygrolycosa rubrofasciata*. 34 p. (108 p.). Yhteenveto 2 p. 1999.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 78 VIROLAINEN, KAIJA, Selection of nature reserve networks. - Luonnonsuojelualueiden valinta. 28 p. (87 p.). Yhteenveto 1 p. 1999.
- 79 SELIN, PIRKKO, Turvevarojen teollinen käyttö ja suopohjan hyödyntäminen Suomessa. - Industrial use of peatlands and the re-use of cut-away areas in Finland. 262 p. Foreword 3 p. Executive summary 9 p. 1999.
- 80 LEPPÄNEN, HARRI, The fate of resin acids and resin acid-derived compounds in aquatic environment contaminated by chemical wood industry. - Hartsihappojen ja hartsihappoppe- räisten yhdisteiden ympäristökohtalo kemiallisen puunjalostusteollisuuden likaamissa vesistöissä. 45 p. (149 p.). Yhteenveto 2 p. 1999.
- 81 LINDSTRÖM, LEENA, Evolution of conspicuous warning signals. - Näkyvien varoitussignaalien evoluutio. 44 p. (96 p.). Yhteenveto 3 p. 2000.
- 82 MATTILA, ELISA, Factors limiting reproductive success in terrestrial orchids. - Kämmeköiden lisääntymismenestystä rajoittavat tekijät. 29 p. (95 p.). Yhteenveto 2 p. 2000.
- 83 KARELS, AARNO, Ecotoxicity of pulp and paper mill effluents in fish. Responses at biochemical, individual, population and community levels. - Sellu- ja paperiteollisuuden jätevesien ekotoksisuus kaloille. Tutkimus kalojen biokemiallisista, fysiologisista sekä populaatio- ja yhteisövasteista. 68 p. (177 p.). Yhteenveto 1 p. Samenvatting 1 p. 2000.
- 84 AALTONEN, TUULA, Effects of pulp and paper mill effluents on fish immune defence. - Met- säteollisuuden jätevesien aiheuttamat immunologiset muutokset kaloissa. 62 p. (125 p.). 2000.
- 85 HELENIUS, MERJA, Aging-associated changes in NF-kappa B signaling. - Ikääntymisen vaikutus NF-kappa B:n signalointiin. 75 p. (143 p.). Yhteenveto 2 p. 2000.
- 86 HUOVINEN, PIRJO, Ultraviolet radiation in aquatic environments. Underwater UV penetration and responses in algae and zooplankton. - Ultraviolettisaiteilyn vedenalain tunkeutuminen ja sen vaikutukset leviin ja eläinplanktoniin. 52 p. (145 p.). Yhteenveto 2 p. 2000.
- 87 PÄÄKKÖNEN, JARI-PEKKA, Feeding biology of burbot, *Lota lota* (L.): Adaptation to profundal lifestyle? - Mateen, *Lota lota* (L), ravinnon- käytön erityispiirteet: sopeumia pohja- elämään? 33 p. (79 p.). Yhteenveto 2 p. 2000.
- 88 LAASONEN, PEKKA, The effects of stream habit restoration on benthic communities in boreal headwater streams. - Koskikunnostuksen vaikutus jokien pohjaeläimistöön. 32 p. (101 p.). Yhteenveto 2 p. 2000.
- 89 PASONEN, HANNA-LEENA, Pollen competition in silver birch (*Betula pendula* Roth). An evolutionary perspective and implications for commercial seed production. - Siitepölykilpailu koivulla. 41 p. (115 p.). Yhteenveto 2 p. 2000.
- 90 SALMINEN, ESA, Anaerobic digestion of solid poultry slaughterhouse by-products and wastes. - Siipikarjateurastuksen sivutuotteiden ja jätteiden anaerobinen käsittely. 60 p. (166 p.). Yhteenveto 2 p. 2000.
- 91 SALO, HARRI, Effects of ultraviolet radiation on the immune system of fish. - Ultraviolettisaiteilyn vaikutus kalan immunologiseen puolustusjärjestelmään. 61 p. (109 p.). Yhteenveto 2 p. 2000.
- 92 MUSTAJÄRVI, KAISA, Genetic and ecological consequences of small population size in *Lychnis viscaria*. - Geneettisten ja ekologisten tekijöiden vaikutus pienten mäkitervakko- populaatioiden elinkykyyn. 33 p. (124 p.). Yhteenveto 3 p. 2000.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 93 TIKKA, PÄIVI, Threatened flora of semi-natural grasslands: preservation and restoration. - Niittykasvillisuuden säilyttäminen ja ennallistaminen. 35 p. (105 p.). Yhteenveto 2 p. 2001.
- 94 SIITARI, HELI, Ultraviolet sensitivity in birds: consequences on foraging and mate choice. - Lintujen ultravioletin ekologinen merkitys ravinnon- ja puolisonvalinnassa. 31 p. (90 p.). Yhteenveto 2 p. 2001.
- 95 VERTAINEN, LAURA, Variation in life-history traits and behaviour among wolf spider (*Hygrolycosa rubrofasciata*) populations. - Populaatioiden väliset erot rummuttavan hämähäkin *Hygrolycosa rubrofasciata* kasvussa ja käyttäytymisessä. 37 p. (117 p.) Yhteenveto 2 p. 2001.
- 96 HAAPALA, ANTTI, The importance of particulate organic matter to invertebrate communities of boreal woodland streams. Implications for stream restoration. - Hiukkasmaisen orgaanisen aineksen merkitys pohjoisten metsäjokien pohja-eläinyhteisöille - huomioita virtavesien kunnostushankkeisiin. 35 p. (127 p.) Yhteenveto 2 p. 2001.
- 97 NISSINEN, LIISA, The collagen receptor integrins - differential regulation of their expression and signaling functions. - Kollageeniin sitoutuvat integriinit - niiden toisistaan eroava säätely ja signalointi. 67 p. (125 p.) Yhteenveto 1 p. 2001.
- 98 AHLROTH, MERVI, The chicken avidin gene family. Organization, evolution and frequent recombination. - Kanan avidiini-geeniperhe. Organisaatio, evoluutio ja tiheä rekombinaatio. 73 p. (120 p.) Yhteenveto 2 p. 2001.
- 99 HYÖTYLÄINEN, TARJA, Assessment of ecotoxicological effects of creosote-contaminated lake sediment and its remediation. - Kreosotilla saastuneen järvisedimentin ekotoksikologisen riskin ja kunnostuksen arviointi. 59 p. (132 p.) Yhteenveto 2 p. 2001.
- 100 SULKAVA, PEKKA, Interactions between faunal community and decomposition processes in relation to microclimate and heterogeneity in boreal forest soil. - Maaperän eliöyhteisön ja hajotusprosessien väliset vuorovaikutukset suhteessa mikroilmastoon ja laikut-taisuuteen. 36 p. (94 p.) Yhteenveto 2 p. 2001.
- 101 LAITINEN, OLLI, Engineering of physicochemical properties and quaternary structure assemblies of avidin and streptavidin, and characterization of avidin related proteins. - Avidiinin ja streptaviidiinin kvaternäärirakenteen ja fysiokemiallisten ominaisuuksien muokkaus sekä avidiinin kaltaisten proteiinien karakterisointi. 81 p. (126 p.) Yhteenveto 2 p. 2001.
- 102 LYYTINEN, ANNE, Insect coloration as a defence mechanism against visually hunting predators. - Hyönteisten väritys puolustuksessa vihollisia vastaan. 44 p. (92 p.) Yhteenveto 3 p. 2001.
- 103 NIKKILÄ, ANNA, Effects of organic material on the bioavailability, toxicokinetics and toxicity of xenobiotics in freshwater organisms. - Orgaanisen aineksen vaikutus vierasaineiden biosaatavuuteen, toksikokinetiikkaan ja toksisuuteen vesieliöillä. 49 p. (102 p.) Yhteenveto 3 p. 2001.
- 104 LIIRI, MIRA, Complexity of soil faunal communities in relation to ecosystem functioning in coniferous forest soil. A disturbance oriented study. - Maaperän hajottajaeliöstön monimuotoisuuden merkitys metsäekosysteemin toiminnassa ja häiriön-siedossa. 36 p. (121 p.) Yhteenveto 2 p. 2001.
- 105 KOSKELA, TANJA, Potential for coevolution in a host plant - holoparasitic plant interaction. - Isäntäkasvin ja täysloiskasvin välinen vuoro-vaikutus: edellytyksiä koevoluutiolle? 44 p. (122 p.) Yhteenveto 3 p. 2001.
- 106 LAPPIVAARA, JARMO, Modifications of acute physiological stress response in whitefish after prolonged exposures to water of anthropogenically impaired quality. - Ihmistoiminnan aiheuttaman veden laadun heikentymisen vaikutukset planktonsiian fysiologisessa stressivasteessa. 46 p. (108 p.) Yhteenveto 3 p. 2001.
- 107 ECCARD, JANA, Effects of competition and seasonality on life history traits of bank voles. - Kilpailun ja vuodenaikaisvaihtelun vaikutus metsämyyrän elinkiertopiirteisiin. 29 p. (115 p.) Yhteenveto 2 p. 2002.
- 108 NIEMINEN, JOUNI, Modelling the functioning of experimental soil food webs. - Kokeellisten maaperäravintoverkkojen toiminnan mallintaminen. 31 p. (111 p.) Yhteenveto 2 p. 2002.
- 109 NYKÄNEN, MARKO, Protein secretion in *Trichoderma reesei*. Expression, secretion and maturation of cellobiohydrolase I, barley cysteine proteinase and calf chymosin in Rut-C30. - Proteiinien erittyminen *Trichoderma reesei*ssä. Sellobiohydraasi I:n, ohran kysteiini-proteiinaasin sekä vasikan kymosiinin ilmeneminen, erittyminen ja kypsyminen Rut-C30-mutanttikannassa. 107 p. (173 p.) Yhteenveto 2 p. 2002.
- 110 TIIROLA, MARJA, Phylogenetic analysis of bacterial diversity using ribosomal RNA gene sequences. - Ribosomaalisen RNA-geenin sekvenssien käyttö bakteeridiver-siteetin fylogeneettisessä analyysissä. 75 p. (139 p.) Yhteenveto 2 p. 2002.
- 111 HONKAVAARA, JOHANNA, Ultraviolet cues in fruit-frugivore interactions. - Ultravioletin ekologinen merkitys hedelmiä syövien eläinten ja hedelmäkasvien välisissä vuoro-vaikutussuhteissa. 27 p. (95 p.) Yhteenveto 2 p. 2002.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 112 MARTTILA, ARI, Engineering of charge, biotin-binding and oligomerization of avidin: new tools for avidin-biotin technology. - Avidiinin varauksen, biotiininsitomisen sekä oligomerisaation muokkaus: uusia työkaluja avidiini-biotiiniteknologiaan. 68 p. (130 p.) Yhteenveto 2 p. 2002.
- 113 JOKELA, JARI, Landfill operation and waste management procedures in the reduction of methane and leachate pollutant emissions from municipal solid waste landfills. - Kaatopaikan operoinnin ja jätteen esikäsittelyn vaikutus yhdyskuntajätteen biohajoamiseen ja tyyppipäästöjen hallintaan. 62 p. (173 p.) Yhteenveto 3 p. 2002.
- 114 RANTALA, MARKUS J., Immunocompetence and sexual selection in insects. - Immunokompetenssi ja seksuaalivalinta hyönteisillä. 23 p. (108 p.) Yhteenveto 1 p. 2002.
- 115 OKSANEN, TUULA, Cost of reproduction and offspring quality in the evolution of reproductive effort. - Lisäntymisen kustannukset ja poikasten laatu lisääntymispanostuksen evoluutiossa. 33 p. (95 p.) Yhteenveto 2 p. 2002.
- 116 HEINO, JANI, Spatial variation of benthic macroinvertebrate biodiversity in boreal streams. Biogeographic context and conservation implications. - Pohjaeläinhyteisöjen monimuotoisuuden spatiaalinen vaihtelu pohjoisissa virtavesissä - eliömaantieteellinen yhteys sekä merkitys jokivesien suojelulle. 43 p. (169 p.) Yhteenveto 3 p. 2002.
- 117 SIIRA-PIETIKÄINEN, ANNE, Decomposer community in boreal coniferous forest soil after forest harvesting: mechanisms behind responses. - Pohjoisen havumetsämaan hajottajayhteisö hakkuiden jälkeen: muutoksiin johtavat mekanismit. 46 p. (142 p.) Yhteenveto 3 p. 2002.
- 118 KORTET, RAINE, Parasitism, reproduction and sexual selection of roach, *Rutilus rutilus* L. - Loisten ja taudinaiheuttajien merkitys kalan lisääntymisessä ja seksuaalivalinnassa. 37 p. (111 p.) Yhteenveto 2 p. 2003.
- 119 SUVILAMPI, JUHANI, Aerobic wastewater treatment under high and varying temperatures - thermophilic process performance and effluent quality. - Jätevesien käsittely korkeissa ja vaihtelevissa lämpötiloissa. 59 p. (156 p.) Yhteenveto 2 p. 2003.
- 120 PÄIVINEN, JUSSI, Distribution, abundance and species richness of butterflies and myrmecophilous beetles. - Perhosten ja muurahaispesissä elävien kovakuoriaisten levinneisyys, runsaus ja lajistollinen monimuotoisuus 44 p. (155 p.) Yhteenveto 2 p. 2003.
- 121 PAAVOLA, RIKU, Community structure of macroinvertebrates, bryophytes and fish in boreal streams. Patterns from local to regional scales, with conservation implications. - Selkärangattomien, vesisammalten ja kalojen yhteisö rakenne pohjoisissa virtavesissä - säännönmukaisuudet paikallisesta mittakaavasta alueelliseen ja luonnonsuojellukseen merkitys. 36 p. (121 p.) Yhteenveto 3 p. 2003.
- 122 SUIKKANEN, SANNA, Cell biology of canine parvovirus entry. - Koiran parvovirusinfektion alkuvaiheiden solubiologia. 88 p. (135 p.) Yhteenveto 3 p. 2003.
- 123 AHTIAINEN, JARI JUHANI, Condition-dependence of male sexual signalling in the drumming wolf spider *Hygrolycosa rubrofasciata*. - Koiraan seksuaalisen signaalin kunto riippuvuus rummuttavalla susihämähäkillä *Hygrolycosa rubrofasciata*. 31 p. (121 p.) Yhteenveto 2 p. 2003.
- 124 KAPARAJU, PRASAD, Enhancing methane production in a farm-scale biogas production system. - Metaanintuoton tehostaminen tilakohtaisessa biokaasuntuotantojärjestelmässä. 84 p. (224 p.) Yhteenveto 2 p. 2003.
- 125 HÄKKINEN, JANI, Comparative sensitivity of boreal fishes to UV-B and UV-induced phototoxicity of retene. - Kalojen varhaisvaiheiden herkkyys UV-B säteilylle ja reteenin UV-valoindusoituvalle toksisuudelle. 58 p. (134 p.) Yhteenveto 2 p. 2003.
- 126 NORDLUND, HENRI, Avidin engineering; modification of function, oligomerization, stability and structure topology. - Avidiinin toiminnan, oligomerisaation, kestävyden ja rakennetopologian muokkaaminen. 64 p. (104 p.) Yhteenveto 2 p. 2003.
- 127 MARJOMÄKI, TIMO J., Recruitment variability in vendace, *Coregonus albula* (L.), and its consequences for vendace harvesting. - Muikun, *Coregonus albula* (L.), vuosiluokkien runsauden vaihtelu ja sen vaikutukset kalastukseen. 66 p. (155 p.) Yhteenveto 2 p. 2003.
- 128 KILPIMAA, JANNE, Male ornamentation and immune function in two species of passerines. - Koiraan ornamentit ja immuunipuolustus varpuslinnuilla. 34 p. (104 p.) Yhteenveto 1 p. 2004.
- 129 PÖNNIÖ, TIIA, Analyzing the function of nuclear receptor Nor-1 in mice. - Hiiren tumareseptori Nor-1:n toiminnan tutkiminen. 65 p. (119 p.) Yhteenveto 2 p. 2004.
- 130 WANG, HONG, Function and structure, subcellular localization and evolution of the encoding gene of pentachlorophenol 4-monooxygenase in sphingomonads. 56 p. (90 p.) 2004.
- 131 YLÖNEN, OLLI, Effects of enhancing UV-B irradiance on the behaviour, survival and metabolism of coregonid larvae. - Lisääntyvän UV-B säteilyn vaikutukset siikakalojen poikasten käyttäytymiseen, kuolleisuuteen ja metaboliaan. 42 p. (95 p.) Yhteenveto 2 p. 2004.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 132 KUMPULAINEN, TOMI, The evolution and maintenance of reproductive strategies in bag worm moths (Lepidoptera: Psychidae). - Lisääntymisstrategioiden evoluutio ja säilyminen pussikehrääjillä (Lepidoptera: Psychidae). 42 p. (161 p.) Yhteenveto 3 p. 2004.
- 133 OJALA, KIRSI, Development and applications of baculoviral display techniques. - Bakulovirus display -tekniikoiden kehittäminen ja sovellukset. 90 p. (141 p.) Yhteenveto 3 p. 2004.
- 134 RANTALAINEN, MINNA-LIISA, Sensitivity of soil decomposer communities to habitat fragmentation - an experimental approach. - Metsämaaperän hajottajayhteisön vasteet elinympäristön pirstaloitumiseen. 38 p. (130 p.) Yhteenveto 2 p. 2004.
- 135 SAARINEN, MARI, Factors contributing to the abundance of the ergasilid copepod, *Paraergasilus rylovi*, in its freshwater molluscan host, *Anodonta piscinalis*. - *Paraergasilus rylovi* -loisäyriäisen esiintymiseen ja runsauteen vaikuttavat tekijät *Anodonta piscinalis* -pikkujärvisimpukassa. 47 p. (133 p.) Yhteenveto 4 p. 2004.
- 136 LILJA, JUHA, Assessment of fish migration in rivers by horizontal echo sounding: Problems concerning side-aspect target strength. - Jokeen vaeltavien kalojen laskeminen sivuttaisuuntaisella kaikuluotauksella: sivuaspektikohdevoimakkuuteen liittyviä ongelmia. 40 p. (82 p.) Yhteenveto 2 p. 2004.
- 137 NYKVIST, PETRI, Integrins as cellular receptors for fibril-forming and transmembrane collagens. - Integriinit reseptoreina fibrillaarisille ja transmembraanisille kollageeneille. 127 p. (161 p.) Yhteenveto 3 p. 2004.
- 138 KOIVULA, NIINA, Temporal perspective of humification of organic matter. - Orgaanisen aineen humuistuminen tarkasteltuna ajan funktiona. 62 p. (164 p.) Yhteenveto 2 p. 2004.
- 139 KARVONEN, ANSSI, Transmission of *Diplostomum spathaceum* between intermediate hosts. - *Diplostomum spathaceum* -loisen siirtyminen kotilo- ja kalaisännän välillä. 40 p. (90 p.) Yhteenveto 2 p. 2004.
- 140 NYKÄNEN, MARI, Habitat selection by riverine grayling, *Thymallus thymallus* L. - Harjuksen (*Thymallus thymallus* L.) habitaahtinvalinta virtavesissä. 40 p. (102 p.) Yhteenveto 3 p. 2004.
- 141 HYNYNEN, JUHANI, Anthropogenic changes in Finnish lakes during the past 150 years inferred from benthic invertebrates and their sedimentary remains. - Ihmistoiminnan aiheuttamat kuormitusmuutokset suomalaisissa järvisä viimeksi kuluneiden 150 vuoden aikana tarkasteltuina pohjaeläinyhteisöjen avulla. 45 p. (221 p.) Yhteenveto 3 p. 2004.
- 142 PYLKKÖ, PÄIVI, Atypical *Aeromonas salmonicida* -infection as a threat to farming of arctic charr (*Salvelinus alpinus* L.) and european grayling (*Thymallus thymallus* L.) and putative means to prevent the infection. - Epätyyppinen *Aeromonas salmonicida* -bakteeritartunta uhkana harjukselle (*Thymallus thymallus* L.) ja nierialle (*Salvelinus alpinus* L.) laitoskasvatuksessa ja mahdollisia keinoja tartunnan ennaltaehkäisyyn. 46 p. (107 p.) Yhteenveto 2 p. 2004.
- 143 PUURTINEN, MIKAEL, Evolution of hermaphroditic mating systems in animals. - Kaksineuvoisten lisääntymisstrategioiden evoluutio eläimillä. 28 p. (110 p.) Yhteenveto 3 p. 2004.
- 144 TOLVANEN, OUTI, Effects of waste treatment technique and quality of waste on bioaerosols in Finnish waste treatment plants. - Jätteenkäsittelytekniikan ja jätelaadun vaikutus bioaerosolipitoisuuksiin suomalaisilla jätteenkäsittelylaitoksilla. 78 p. (174 p.) Yhteenveto 4 p. 2004.
- 145 BOADI, KWASI OWUSU, Environment and health in the Accra metropolitan area, Ghana. - Accran (Ghana) suurkaupunkialueen ympäristö ja terveys. 33 p. (123 p.) Yhteenveto 2 p. 2004.
- 146 LUKKARI, TUOMAS, Earthworm responses to metal contamination: Tools for soil quality assessment. - Lierojen vasteet metallialtistukseen: käyttömahdollisuudet maaperän tilan arvioinnissa. 64 p. (150 p.) Yhteenveto 3 p. 2004.
- 147 MARTTINEN, SANNA, Potential of municipal sewage treatment plants to remove bis(2-ethylhexyl) phthalate. - Bis-(2-etyyliheksyyli)ftalaatin poistaminen jätevesistä yhdyskuntajätevedenpuhdistamoilla. 51 p. (100 p.) Yhteenveto 2 p. 2004.
- 148 KARISOLA, PIILA, Immunological characterization and engineering of the major latex allergen, hevein (Hev b 6.02). - Luonnonkumiallergian pääallergeenin, heveinin (Hev b 6.02), immunologisten ominaisuuksien karakterisointi ja muokkaus. 91 p. (113 p.) Yhteenveto 2 p. 2004.
- 149 BAGGE, ANNA MARIA, Factors affecting the development and structure of monogenean communities on cyprinid fish. - Kidusloisyhteisöjen rakenteeseen ja kehitykseen vaikuttavat tekijät sisävesikaloilla. 25 p. (76 p.) Yhteenveto 1 p. 2005.
- 150 JÄNTTI, ARI, Effects of interspecific relationships in forested landscapes on breeding success in Eurasian treecreeper. - Lajienvälisen suhteiden vaikutus puukiipijän pesintämenestykseen metsäympäristössä. 39 p. (104 p.) Yhteenveto 2 p. 2005.
- 151 TYNKKYNNEN, KATJA, Interspecific interactions and selection on secondary sexual characters in damselflies. - Lajienväliset vuorovaikutukset ja seksuaaliominaisuuksiin kohdistuva valinta sudenkorennoilla. 26 p. (86 p.) Yhteenveto 2 p. 2005.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 152 HAKALAHTI, TEIJA, Studies of the life history of a parasite: a basis for effective population management. - Loisen elinkiertopiirteet: perusta tehokkaalle torjunnalle. 41 p. (90 p.) Yhteenveto 3 p. 2005.
- 153 HYTÖNEN, VESA, The avidin protein family: properties of family members and engineering of novel biotin-binding protein tools. - Avidiini-proteiiniperhe: perheen jäsenten ominaisuuksia ja uusia biotiiniä sitovia proteiiniyökaluja. 94 p. (124 p.) Yhteenveto 2 p. 2005.
- 154 GILBERT, LEONA, Development of biotechnological tools for studying infectious pathways of canine and human parvoviruses. 104 p. (156 p.) 2005.
- 155 SUOMALAINEN, LOTTA-RIINA, *Flavobacterium columnare* in Finnish fish farming: characterisation and putative disease management strategies. - *Flavobacterium columnare* Suomen kalanviljelyssä: karakterisointi ja mahdolliset torjuntamenetelmät. 52 p. (110 p.) Yhteenveto 1 p. 2005.
- 156 VEHNÄINEN, EEVA-RIIKKA, Boreal fishes and ultraviolet radiation: actions of UVR at molecular and individual levels. - Pohjoisen kalat ja ultraviolettisäteily: UV-säteilyn vaikutukset molekyyli- ja yksilötasolla. 52 p. (131 p.) 2005.
- 157 VAINIKKA, ANSSI, Mechanisms of honest sexual signalling and life history trade-offs in three cyprinid fishes. - Rehellisen seksuaalisen signaaloinnin ja elinkiertojen evoluution mekanismit kolmella särkikalalla. 53 p. (123 p.) Yhteenveto 2 p. 2005.
- 158 LUOSTARINEN, SARI, Anaerobic on-site wastewater treatment at low temperatures. Jätevesien kiinteistö- ja kyläkohtainen anaerobinen käsittely alhaisissa lämpötiloissa. 83 p. (168 p.) Yhteenveto 3 p. 2005.
- 159 SEPPÄLÄ, OTTO, Host manipulation by parasites: adaptation to enhance transmission? Loisten kyky manipuloida isäntiään: sopeuma transmission tehostamiseen? 27 p. (67 p.) Yhteenveto 2 p. 2005.
- 160 SUURINIEMI, MIIA, Genetics of children's bone growth. - Lasten luuston kasvun genetiikka. 74 p. (135 p.) Yhteenveto 3 p. 2006.
- 161 TOIVOLA, JOUNI, Characterization of viral nanoparticles and virus-like structures by using fluorescence correlation spectroscopy (FCS). - Virus-nanopartikkelien sekä virusten kaltaisten rakenteiden tarkastelu fluoresenssi korrelaatio spektroskopiolla. 74 p. (132 p.) Yhteenveto 2 p. 2006.
- 162 KLEMME, INES, Polyandry and its effect on male and female fitness. - Polyandria ja sen vaikutukset koiraan ja naaraan kelpoisuuteen 28 p. (92 p.) Yhteenveto 2 p. 2006.
- 163 LEHTOMÄKI, ANNIMARI, Biogas production from energy crops and crop residues. - Energia-kasvien ja kasvijätteiden hyödyntäminen biokaasun tuotannossa. 91 p. (186 p.) Yhteenveto 3 p. 2006.
- 164 ILMARINEN, KATJA, Defoliation and plant-soil interactions in grasslands. - Defoliaatio ja kasvien ja maaperän väliset vuorovaikutukset niittyekosysteemeissä. 32 p. (111 p.) Yhteenveto 2 p. 2006.
- 165 LOEHR, JOHN, Thinhorn sheep evolution and behaviour. - Ohutsarvilampaiden evoluutio ja käyttäytyminen. 27 p. (89 p.) Yhteenveto 2 p. 2006.
- 166 PAUKKU, SATU, Cost of reproduction in a seed beetle: a quantitative genetic perspective. - Lisääntymisen kustannukset jyväkuoriaisella: kvantitatiivisen genetiikan näkökulma. 27 p. (84 p.) Yhteenveto 1 p. 2006.
- 167 OJALA, KATJA, Variation in defence and its fitness consequences in aposematic animals: interactions among diet, parasites and predators. - Puolustuskyvyn vaihtelu ja sen merkitys aposemaattisten eläinten kelpoisuuteen: ravinnon, loisten ja saalistajien vuorovaikutus. 39 p. (121 p.) Yhteenveto 2 p. 2006.
- 168 MATILAINEN, HELI, Development of baculovirus display strategies towards targeting to tumor vasculature. - Syövän suonitukseen kohdentuvien bakulovirus display-vektorien kehittäminen. 115 p. (167 p.) Yhteenveto 2 p. 2006.
- 169 KALLIO, EVA R., Experimental ecology on the interaction between the Puumala hantavirus and its host, the bank vole. - Kokeellista ekologiaa Puumala-viruksen ja metsämyyrän välisestä vuorovaikutussuhteesta. 30 p. (75 p.) Yhteenveto 2 p. 2006.
- 170 PIHLAJA, MARJO, Maternal effects in the magpie. - Harakan äitivaikutukset. 39 p. (126p.) Yhteenveto 1 p. 2006.
- 171 IHALAINEN, EIRA, Experiments on defensive mimicry: linkages between predator behaviour and qualities of the prey. - Varoitussignaalin jäljittely puolustusstrategiana: kokeita petosaalis-suhteista. 37 p. (111 p.) Yhteenveto 2 p. 2006.
- 172 LÓPEZ-SEPULCRE, ANDRÉS, The evolutionary ecology of space use and its conservation consequences. - Elintilan käytön ja reviiirikäyttäytymisen evoluutioekologia luonnonsuojellullisine seuraamuksineen. 32 p. (119 p.) Yhteenveto 2 p. 2007.
- 173 TULLA, MIRA, Collagen receptor integrins: evolution, ligand binding selectivity and the effect of activation. - Kollageenireseptori-integriinien evoluutio, ligandin sitomisvalikoivuus ja aktivaation vaikutus. 67 p. (129 p.) Yhteenveto 2 p. 2007.
- 174 SINISALO, TUULA, Diet and foraging of ringed seals in relation to helminth parasite assemblages. - Perämeren ja Saimaan norpan suolistolohyönteisöt ja niiden hyödyntäminen hylkeen yksilöllisen ravintoekologian selvittämisessä. 38 p. (84 p.) Yhteenveto 2 p. 2007.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 175 TOIVANEN, TERO, Short-term effects of forest restoration on beetle diversity. - Metsien ennallistamisen merkitys kovakuoriaislajiston monimuotoisuudelle. 33 p. (112 p.) Yhteenveto 2 p. 2007.
- 176 LUDWIG, GILBERT, Mechanisms of population declines in boreal forest grouse. - Kanalintukantojen laskuun vaikuttavat tekijät. 48 p. (138 p.) Yhteenveto 2 p. 2007.
- 177 KETOLA, TARMO, Genetics of condition and sexual selection. - Kunnon ja seksuaalivalinnan genetiikka. 29 p. (121 p.) Yhteenveto 2 p. 2007.
- 178 SEPPÄNEN, JANNE-TUOMAS, Interspecific social information in habitat choice. - Lajienvälinen sosiaalinen informaatio habitaatinvalinnassa. 33 p. (89 p.) Yhteenveto 2 p. 2007.
- 179 BANDILLA, MATTHIAS, Transmission and host and mate location in the fish louse *Argulus coregoni* and its link with bacterial disease in fish. - *Argulus coregoni* -kalatäin siirtyminen kalaisäntään, isännän ja parittelukumppanin paikallistaminen sekä loisinnan yhteys kalan bakteeritautiin. 40 p. (100 p.) Yhteenveto 3 p. Zusammenfassung 4 p. 2007.
- 180 MERILÄINEN, PÄIVI, Exposure assessment of animals to sediments contaminated by pulp and paper mills. - Sellu- ja paperiteollisuuden saastuttamat sedimentit altistavana tekijänä vesieläimille. 79 p. (169 p.) Yhteenveto 2 p. 2007.
- 181 ROUTTU, JARKKO, Genetic and phenotypic divergence in *Drosophila virilis* and *D. montana*. - Geneettinen ja fenotyyppinen erilaistuminen *Drosophila virilis* ja *D. montana* lajien mahlakärpäisillä. 34 p. (106 p.) Yhteenveto 1 p. 2007.
- 182 BENESH, DANIEL P., Larval life history, transmission strategies, and the evolution of intermediate host exploitation by complex life-cycle parasites. - Väkäkärsämatotoukkien elinkierto- ja transmissiostrategiat sekä välisännän hyväksikäytön evoluutio. 33 p. (88 p.) Yhteenveto 1 p. 2007.
- 183 TAIPALE, SAMI, Bacterial-mediated terrestrial carbon in the foodweb of humic lakes. - Bakteerivälitteisen terrestrisen hiilen merkitys humusjärvien ravintoketjussa. 61 p. (131 p.) Yhteenveto 5 p. 2007.
- 184 KILJUNEN, MIKKO, Accumulation of organochlorines in Baltic Sea fishes. - Organoklooriyhdisteiden kertyminen Itämeren kaloihin. 45 p. (97 p.) Yhteenveto 3 p. 2007.
- 185 SORMUNEN, KAI MARKUS, Characterisation of landfills for recovery of methane and control of emissions. - Kaatopaikkojen karakterisointi metaanipotentiaalin hyödyntämiseksi ja päästöjen vähentämiseksi. 83 p. (157 p.) Yhteenveto 2 p. 2008.
- 186 HILTUNEN, TEPPO, Environmental fluctuations and predation modulate community dynamics and diversity. - Ympäristön vaihtelut ja saalistus muokkaavat yhteisön dynamiikkaa ja diversiteettiä. 33 p. (100 p.) Yhteenveto 2 p. 2008.
- 187 SYVÄRANTA, JARI, Impacts of biomanipulation on lake ecosystem structure revealed by stable isotope analysis. - Biomanipulaation vaikutukset järviökosysteemin rakenteeseen vakaiden isotooppien avulla tarkasteltuna. 46 p. (105 p.) Yhteenveto 4 p. 2008.
- 188 MATTILA, NIINA, Ecological traits as determinants of extinction risk and distribution change in Lepidoptera. - Perhosten uhanalaisuuteen vaikuttavat ekologiset piirteet. 21 p. (67 p.) Yhteenveto 1 p. 2008.
- 189 UPLA, PAULA, Integrin-mediated entry of echovirus 1. - Echovirus 1:n integriini-välitteinen sisäänmeno soluun. 86 p. (145 p.) Yhteenveto 2 p. 2008.
- 190 KESKINEN, TAPIO, Feeding ecology and behaviour of pikeperch, Sander lucioperca (L.) in boreal lakes. - Kuhan (Sander lucioperca (L.)) ravinnonkäyttö ja käyttäytyminen boreaalisissa järvissä. 54 p. (136 p.) Yhteenveto 3 p. 2008.
- 191 LAAKKONEN, JOHANNA, Intracellular delivery of baculovirus and streptavidin-based vectors *in vitro* - towards novel therapeutic applications. - Bakulovirus ja streptavidiini geeninsiirtovektoreina ihmisen soluissa. 81 p. (142 p.) Yhteenveto 2 p. 2008.
- 192 MICHEL, PATRIK, Production, purification and evaluation of insect cell-expressed proteins with diagnostic potential. - Diagnostisesti tärkeiden proteiinien tuotto hyönteissolussa sekä niiden puhdistus ja karakterisointi. 100 p. (119 p.) Yhteenveto 2 p. 2008.
- 193 LINDSTEDT, CARITA, Maintenance of variation in warning signals under opposing selection pressures. - Vastakkaiset evolutiiviset valintapaineet ylläpitävät vaihtelua varoitussignaalinnissa. 56 p. (152 p.) Yhteenveto 2 p. 2008.
- 194 BOMAN, SANNA, Ecological and genetic factors contributing to invasion success: The northern spread of the Colorado potato beetle (*Leptinotarsa decemlineata*). - Ekologisten ja geneettisten tekijöiden vaikutus koloradonkuoriaisen (*Leptinotarsa decemlineata*) leviämismenestykseen. 50 p. (113 p.) Yhteenveto 3 p. 2008.
- 195 MÄKELÄ, ANNA, Towards therapeutic gene delivery to human cancer cells. Targeting and entry of baculovirus. - Kohti terapeuttista geeninsiirtoa: bakuloviruksen kohdennus ja sisäänmeno ihmisen syöpäsoluihin. 103 p. (185 p.) Yhteenveto 2 p. 2008.
- 196 LEBIGRE, CHRISTOPHE, Mating behaviour of the black grouse. Genetic characteristics and physiological consequences. - Teeren pariutumiskäyttäytyminen. Geneettiset tekijät ja fysiologiset seuraukset. 32 p. (111 p.) Yhteenveto 2 p. 2008.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 197 KAKKONEN, ELINA, Regulation of raft-derived endocytic pathways – studies on echovirus 1 and baculovirus. - Echovirus 1:n ja bakuloviruksen soluun sisäänmenon reitit ja säätely. 96 p. (159 p.) Yhteenveto 2 p. 2009.
- 198 TENHOLA-ROININEN, TEIJA, Rye doubled haploids – production and use in mapping studies. - Rukiin kaksoishaploidit – tuotto ja käyttö kartoituksessa. 93 p. (164 p.) Yhteenveto 3 p. 2009.
- 199 TREBATICKÁ, LENKA, Predation risk shaping individual behaviour, life histories and species interactions in small mammals. - Petoriskin vaikutus yksilön käyttäytymiseen, elinkiertopiirteisiin ja yksilöiden välisiin suhteisiin. 29 p. (91 p.) Yhteenveto 3 p. 2009.
- 200 PIETIKÄINEN, ANNE, Arbuscular mycorrhiza, resource availability and belowground interactions between plants and soil microbes. - Arbuskelimykorrhiza, resurssien saatavuus ja maanalaiset kasvien ja mikrobien väliset vuorovaikutukset. 38 p. (119 p.) Yhteenveto 2 p. 2009.
- 201 AROVIITA, JUKKA, Predictive models in assessment of macroinvertebrates in boreal rivers. - Ennustavat mallit jokien pohjaeläimistön tilan arvioinnissa. 45 p. (109 p.) Yhteenveto 3 p. 2009.
- 202 RASI, SAIJA, Biogas composition and upgrading to biomethane. - Biokaasun koostumus ja puhdistaminen biometaaniksi. 76 p. (135 p.) Yhteenveto 3 p. 2009.
- 203 PAKKANEN, KIRSI, From endosomes onwards. Membranes, lysosomes and viral capsid interactions. - Endosomeista eteenpäin. Lipidikalvoja, lysosomeja ja viruskapsidin vuorovaikutuksia. 119 p. (204 p.) Yhteenveto 2 p. 2009.
- 204 MARKKULA, EVELIINA, Ultraviolet B radiation induced alterations in immune function of fish, in relation to habitat preference and disease resistance. - Ultravioletti B -säteilyn vaikutus kalan taudinvastustuskykyyn ja immunologisen puolustusjärjestelmän toimintaan. 50 p. (99 p.) Yhteenveto 2 p. 2009.
- 205 IHALAINEN, TEEMU, Intranuclear dynamics in parvovirus infection. - Tumansisäinen dynamiikka parvovirus infektiossa. 86 p. (152 p.) Yhteenveto 3 p. 2009.
- 206 KUNTTU, HEIDI, Characterizing the bacterial fish pathogen *Flavobacterium columnare*, and some factors affecting its pathogenicity. - Kalapato-geeni *Flavobacterium columnare* -bakteerin ominaisuuksia ja patogeenisuuteen vaikuttavia tekijöitä. 69 p. (120 p.) Yhteenveto 3 p. 2010.
- 207 KOTILAINEN, TITTA, Solar UV radiation and plant responses: Assessing the methodological problems in research concerning stratospheric ozone depletion. - Auringon UV-säteily ja kasvien vasteet: otsonikatoon liittyvien tutkimusten menetelmien arviointia. 45 p. (126 p.) Yhteenveto 2 p. 2010.