Jaana Haapala

Mire plants and carbon dioxide dynamics under increased tropospheric ozone concentration and UV-B radiation

UNIVERSITY OF
EASTERN FINLAND

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Academic Dissertation
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ABSTRACT

The background ozone concentration has more than doubled since the beginning of the 20th century in the northern hemisphere and this trend has been predicted to continue in the near future. At the same time, depletion of the stratospheric ozone layer has led to increased UV-B radiation levels in the polar regions. Increased tropospheric ozone concentrations and UV-B radiation are known to affect plant photosynthesis, growth and the soil microbial community. However, little is known about their long-term effects on ecosystem level carbon dioxide (CO_2) dynamics. This thesis assesses the long-term effects of moderately elevated ozone concentration or supplemental UV-B radiation on the photosynthetic capacity of selected mire plant species and on ecosystem level CO_2 exchange. The presented results were attained from two multi-year experiments; from a four-year free air ozone exposure study with fen microcosms and from a three-year UV-B exposure study on a natural fen.

In the ozone experiment, only high ozone levels occurring in early summer affected the photosynthesis related parameters of the studied sedge, *Eriophorum vaginatum*. Furthermore, ecosystem level gross photosynthesis was decreased in the first growing season under supplemental ozone. However, during the following years, an opposite trend was detected due to the slight increase in the sedge leaf density in the ozone treatment. The effects of supplemental UV-B radiation on a natural fen were negligible. No significant effect on the plant cell fine structure or plant photosynthesis could be detected. At the ecosystem level, the instantaneous ecosystem dark respiration was slightly lower in the UV-B treatment. However, the change was statistically significant only in the third year, when a rapid drawdown of the water-table caused an anomalous respiration peak in all treatments.

In conclusion, neither of the studied stressors had any drastic effect on the net ecosystem CO_2 exchange over the long-term. Only the high springtime ozone concentrations transiently

decreased the plant photosynthetic capacity and caused short-term ecosystem level changes. However, the long-term effects of both stressors differed greatly from the initial effects detected in the first study year and were very dependent on other prevailing environmental conditions. On the basis of these results it seems unlikely that the predicted increase in the background ozone concentration or the future levels of UV-B radiation would significantly decrease the net CO_2 uptake of northern fen ecosystems.

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CAB Thesaurus: Arctic regions; carbon dioxide; chloroplasts; *Eriophorum vaginatum*; net ecosystem exchange; ozone; ozone depletion; peatlands; fens; photosynthesis; respiration; leaves; *Sphagnum*; transmission electron microscopy; ultraviolet radiation; vegetation; cell ultrastructure

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Acknowledgements

LIST OF ABBREVIATIONS

A	Carbon dioxide assimilation
A_{sat}	Carbon dioxide assimilation in light saturated conditions
AOT_{40}	Accumulated ozone exposure over a threshold of 40 parts per billion
a.s.l.	Above sea level
Chl-a	Chlorophyll a
Chl-b	Chlorophyll b
ClO	Chlorine oxide
CO	Carbon monoxide
CO_2	Carbon dioxide
F_m	Maximal fluorescence level in dark-adapted state
F_0	Minimal fluorescence level in dark-adapted state
F_v	Variable fluorescence (F_m-F_0)
F_v/F_m	Maximum quantum efficiency of PSII photochemistry
H_2O_2	Hydrogen peroxide
NEE	Net ecosystem CO_2 exchange
NO_x	Nitrogen oxides
O_3	Ozone
P_G	Gross photosynthesis
PAR	Photosynthetically active radiation, wavelength 400-700 nm
PSII	Photosystem II
R_d	Dark respiration
R_{TOT}	Total ecosystem respiration
ROS	Reactive oxygen species
TEM	Transmission electron microscopy
UV	Ultraviolet radiation
UV-A	Ultraviolet A radiation, wavelength 315-400 nm
UV-B	Ultraviolet B radiation, wavelength 280-315 nm
$UV-B_{CIE}$	Biologically effective UV-B weighted with the erythemal action spectrum of the CIE (International Commission on Illumination) (McKinley & Diffey 1987)
VOC	Volatile organic compound

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I-IV.

I Mörsky S K, Haapala J K, Rinnan R, Saarnio S, Silvola J, Martikainen P J and Holopainen T. Minor effects of long-term ozone exposure on boreal peatland species *Eriophorum vaginatum* and *Sphagnum papillosum*. *Environmental and Experimental Botany 72: 455-463, 2011.*

II Haapala J K, Mörsky S K, Rinnan R, Saarnio S, Martikainen P J, Holopainen T and Silvola J. Long-term effects of ozone on CO_2 exchange in peatland microcosms. *Atmospheric Environment 45: 4002-4007, 2011.*

III Haapala J K, Mörsky S K, Saarnio S, Suokanerva H, Kyrö E, Silvola J and Holopainen T. Long-term effects of elevated UV-B radiation on photosynthesis and ultrastructure of *Eriophorum russeolum* and *Warnstorfia exannulata*. *Science of the Total Environment 409: 370-377, 2010.*

IV Haapala J K, Mörsky S K, Saarnio S, Rinnan R, Suokanerva H, Kyrö E, Latola K, Martikainen P J, Holopainen T and Silvola J. Carbon dioxide balance of a fen ecosystem in northern Finland under elevated UV-B radiation. *Global Change Biology 15: 943-954, 2009.*

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AUTHOR'S CONTRIBUTION

I   Sami K. Mörsky contributed to the field and laboratory work. He also analyzed the anatomy, growth and pigment data and wrote the majority of the manuscript. Jaana Haapala contributed to the laboratory work on the C/N ratio and ultrastructure analysis and analyzed the related data. She also contributed to the writing on the aforementioned sections. Riikka Rinnan and Sanna Saarnio contributed to the writing. Jouko Silvola, Pertti J. Martikainen and Toini Holopainen conceived and designed the study and contributed to the writing. This manuscript will be also used in Sami K. Mörsky's thesis.

II   Jaana Haapala contributed to the data analysis and wrote the paper. Sami K. Mörsky contributed to the field work and writing. Riikka Rinnan and Sanna Saarnio contributed to the writing. Pertti J. Martikainen, Toini Holopainen and Jouko Silvola conceived and designed the study and contributed to the writing.

III   Jaana Haapala contributed to the field and laboratory work, data analysis and wrote the paper. Sami K. Mörsky contributed to the writing and field work. Sanna Saarnio contributed to the writing. Hanne Suokanerva, Esko Kyrö, Toini Holopainen and Jouko Silvola conceived and designed the study and contributed to the writing.

IV   Jaana Haapala contributed to the field work, data analysis and wrote the paper. Sami K. Mörsky, Sanna Saarnio, Riikka Rinnan and Kirsi Latola contributed to the writing. Hanne Suokanerva contributed to the field work and writing. Esko Kyrö, Pertti J. Martikainen, Toini Holopainen and Jouko Silvola conceived and designed the study and contributed to the writing.

Contents

Original publications

1 Introduction

1.1 CARBON CYCLE IN MIRE ECOSYSTEMS

Boreal mires are characterized by a high water table and mire vegetation that is typically dominated by a continuous moss layer, sedges (Cyperaceae Juss.) and dwarf shrubs (Gorham, 1991). The abundance of trees depends on the mire type, mainly as a consequence of water and nutrient availability. Peat mosses (*Sphagnum* sp.) dominate the ground-layer in ombrotrophic bogs and minerotrophic poor fens, whereas true mosses (mostly of the family Amblystegiaceae G. Roth) are more abundant in rich fens (Vitt, 2006).

Although the net primary production in northern mires is low compared to many other ecosystems (Ruimy *et al,.* 1996; Frolking, 1998; Bubier *et al,.* 1999), the decomposition rates are also low because of the high ground water level. When the rate of net primary production exceeds the rate of decomposition, the undecomposed plant material accumulates as peat (Clymo, 1983). However, the annual carbon balance of a mire typically shows great variability between years and the mire ecosystem can alternate between a net sink to a net source of atmospheric carbon (Saarnio *et al,.* 2007). Furthermore, abiotic factors such as leaching of dissolved carbon compounds and peat particles or episodes of fire can reduce peat accumulation.

Atmospheric carbon dioxide (CO_2) is fixed by plant photosynthesis during the growing season. Some of the fixed carbon is released back into the atmosphere through the plant's own maintenance and growth respiration (autotrophic respiration). In vascular plants, a small proportion of photosynthetic products are exuded into the soil through living roots (Farrar *et al,.* 2003) and quickly utilised by the surrounding microbes. The rest is incorporated into the plant biomass and eventually deposited as litter on or into the soil. Decomposition

processes can continue throughout the year and a significant amount of the carbon fixed during the growing season is released from the mire ecosystem during winter (Alm *et al.*, 1997, 1999; Saarnio *et al.*. 2003; Leppälä *et al.*, 2011). In addition to abiotic factors, such as temperature and oxygen availability (water table), the rate of decomposition is dependent on the nutrient availability and the amount and chemical quality of the deposited plant litter (Chapin *et al.*. 2002). For example, high lignin and/ or phenolic compound concentrations decrease the decomposability of the plant litter (Moore & Basiliko, 2006).

In addition to their contribution to CO_2 uptake and above-ground biomass production, living vascular plants have a substantial effect on below-ground processes through their root system. The root system can account for over half of the total plant biomass (Saarinen, 1996; Wallén, 1986) and the living roots transport oxygen and root exudates into the otherwise anoxic peat layers, increasing the microbial activity (Bedford *et al.*, 1991). Although the root exudation accounts for only a few percent of the fixed carbon (Farrar *et al.*, 2003; Saarnio *et al.*, 2004) it provides an important source of fresh nutrients to the soil microbial community (Vasander & Kettunen, 2006). In addition, the aerenchyma tissue of the sedge roots and shoots facilitate transport of methane from the deep peat layers into the atmosphere (Shannon *et al.*, 1996; Thomas *et al.*, 1996). On the other hand, the deep reaching roots deposit plant material directly into the anoxic peat layers where decomposition is slow, thus contributing to carbon accumulation (Saarinen, 1996).

Boreal and subarctic mires cover less than 3% of the global land surface (Joosten 2009) but they have a major role in the global carbon cycle as a long-term store of carbon. The carbon pool in northern mires is estimated to be 270-370 Pg (Turunen *et al.*, 2002), which is equivalent to 35-50% of the present day atmospheric carbon pool (Denman *et al.*, 2007). However, net primary production, biomass allocation and decomposition processes are sensitive to changes in environmental conditions. A plethora of studies have demonstrated that both UV-B radiation and tropospheric ozone have the potential to affect

photosynthesis, growth rate, photosynthate allocation and the secondary chemistry of plants and, consequently, alter the decomposition processes (Andersen, 2003; Ashmore, 2005; Newsham & Robinson, 2009). In the following sections, these effects and their possible contribution to ecosystem level CO_2 balance are discussed.

1.2 EVOLUTION OF THE TROPOSPHERIC OZONE CONCENTRATION

Tropospheric ozone (O_3) is an important air pollutant and greenhouse gas. Although the concentration of stratospheric ozone has been decreasing, the ozone levels in the lower layer of atmosphere, the troposphere, are increasing (Royal Society, 2008). Tropospheric ozone is formed in photochemical reactions involving nitrogen oxides (NO_x), carbon monoxide (CO) and volatile organic compounds (VOC). These precursors originate from both natural biogenic processes and a wide variety of anthropogenic sources, such as burning of fossil fuels, land use change and chemical solvents.

Control of anthropogenic ozone precursor emissions has effectively decreased the peak concentrations in Europe and North America but the back-ground ozone concentration continues to rise (Laurila *et al.*, 2004a) and has more than doubled since the beginning of the 20th century in the northern hemisphere (currently 35-45 ppb). Possible reasons for this are the rise of precursor emissions in the northern hemisphere, international shipping and air traffic (Royal Society, 2008). The rate of increase in annual mean concentrations during the last three decades has been approximately 0.5–2% (Vingarzan, 2004). It has been predicted that the tropospheric ozone concentration in Finland will increase until 2050, although beyond that date the trend in concentration change is less clear (Laurila *et al.*, 2004b).

1.3 STRATOSPHERIC OZONE DEPLETION AND INCREASED UV-B RADIATION

Release of human made halogen source gases has caused increased rates of ozone destruction in the stratosphere since the 1980s. In the stratosphere, these gases can be converted during photochemical reactions into reactive halogen species, which in turn participate in ozone destroying reactions (WMO, 2007). Ozone depletion occurs mainly in the polar regions, where the very low stratospheric temperatures that occur during winter and the relative isolation of the polar air masses provide suitable conditions for the formation of chlorine oxide (ClO). Chlorine oxide is a major component in light dependent reaction cycles that are activated by the returning sun light in late winter and early spring, causing the spring-time decline in the total ozone values.

Ozone depletion has been most notable above the Antarctic, where as much as 60-70% of total ozone was destroyed during springtime in the late 1990s and early 2000s (WMO, 2007). However, significant springtime ozone depletion (monthly mean up to 30-35% compared to the pre-1980 values) has also been observed in the Arctic (ACIA, 2005). After ratification of the Montreal Protocol, the emissions of halogen source gases have decreased. With full compliance with the Protocol and its amendments, the full recovery of total ozone values in the Arctic is expected to occur by the middle of the 21st century (WMO, 2007). However, the recovery of the ozone layer and, in particular, future UV-B radiation levels at the Earth's surface, are affected by several factors other than halogen gas emissions. For example, the potential cooling of the stratosphere as a result of climate warming would cause significant ozone depletion in the mid- and high latitudes (ACIA, 2005). On the other hand, the rise of surface level temperatures would advance the melting of snow cover and expose vegetation to high springtime UV-B radiation levels. As such, it is very difficult to estimate future UV-B radiation levels in the northern high latitudes, particularly

given the naturally high temporal and spatial variability of the arctic ozone values (WMO, 2007; Manney *et al.*, 2011).

1.4 PATHWAYS OF OZONE AND UV-B IMPACTS IN PLANTS

Ozone is a highly reactive oxidant and, therefore, very toxic for vegetation even at comparatively low concentrations. Diffusion of ozone through the plant cuticle is negligible (Pleijel *et al.*, 2004). Therefore, the actual ozone dose received by photosynthesizing plant cells is dependent not only on the ambient ozone concentration but also on the stomatal conductance and the thickness of the boundary layer on the surface of the leaf (Laisk *et al.*, 1989; Ashmore, 2005; Royal Society, 2008). Drought stress usually decreases the internal ozone exposure as the stomata are closed to minimize water loss. In fen ecosystems, stomatal conductance is rarely limited by water deficit even during warm periods during which the highest ozone concentrations usually occur (Royal Society, 2008). Thus, it has been suggested that fen plants would be especially sensitive to ozone (Power & Ashmore, 2002).

Once ozone has reached the extracellular space of the plant mesophyll, it readily reacts with the water and chemicals of the sub-stomatal apoplast forming various reactive compounds, such as hydrogen peroxide (H_2O_2), superoxide (O_2-), hydroxyl radicals ($\cdot OH$) and singlet oxygen (Kanofsky & Sima, 1995; Long & Naidu, 2002), collectively known as reactive oxygen species (ROS). Ozone itself rarely reaches the cell plasmalemma or cytoplasm (Laisk *et al.*, 1989). However, high enough ozone concentrations can overwhelm the antioxidative capacity of the apoplast and induce endogenous production of ROS (oxidative burst) in the cells surrounding the stoma (Kangasjärvi *et al.*, 2005). The endogenous ROS production can continue even after the initial ozone exposure has ended and may eventually lead to the formation of visible lesions (Overmyer *et al.*, 2003; Kangasjärvi *et al.*, 2005). As plants also use ROS as messengers in various development and defence related signal transduction

cascades, the responses to ozone often overlap responses to other stresses such as pathogens, wounding, or even normal senescence (Foyer & Noctor, 2005; Heath, 2008). Therefore, under chronic, low-level ozone exposure, the ozone impact is usually related to reduced photosynthesis and premature senescence (Schraudner *et al.*, 1997).

The effects of realistic UV-B supplementation are often somewhat less dramatic than those of tropospheric ozone. Primary targets of UV-B radiation in plant cells are the proteins and amino acids with aromatic rings, nucleic acids (DNA), lipids (especially those associated with membrane proteins), quinones and, to some extent, photosynthetic pigments (Hollósy, 2002). In addition to the direct damage to the photosynthetic proteins, DNA and a variety of other molecules, UV-B radiation can induce formation of ROS in the chloroplasts as a result of over-excitation of PSII (photo-oxidation), thus causing similar oxidative stress as ozone (Mackerness, 2000). However, plants have a variety of protective and repair processes that effectively alleviate the damage caused by high UV-B radiation (Mackerness, 2000; Hollósy, 2002; Krizek, 2004).

1.5 ULTRASTRUCTURE OF THE PHOTOSYNTHETIC MACHINERY

1.5.1 Ultrastructure of the mesophyll chloroplasts in C3 plants

Ultrastructure analysis provides a sensitive tool for early detection of plant damage (Kivimäenpää, 2003). Chloroplasts are the sites of primary production of plant cells and their proper functioning is crucial for plant growth and survival. Chloroplasts seem to be susceptible to various stress factors and environmental changes (Biswal, 2005b). The size and shape of the chloroplasts differ between species, growth conditions and developmental stage of the mesophyll cell (Kivimäenpää, 2003). In vascular plants, mature, functioning chloroplasts are usually a regular lens shape with a well-ordered thylakoid membrane (Hudák *et al.*, 2005). The thylakoid membrane is organised in chloroplasts either in stacked grana (appressed) or unstacked

stroma lamellae (non-appressed). These two regions of the thylakoid membrane are functionally distinct (Andersson & Andersson, 1980; Albertsson, 1995). The lateral heterogeneity and functional sub-compartmentalization of the thylakoid membranes helps to fine tune the photosynthesis processes (Anderson *et al.*, 2008). Therefore, integrity of the chloroplast membranes is crucial for the efficiency of photosynthesis.

The amount of starch in chloroplasts responds quickly to the rate of photosynthesis, being highest in the afternoon and lowest in early morning (Kivimäenpää *et al.*, 2001). Large starch grains are common in chloroplasts during vigorous growth and indicate the effectiveness of photosynthesis (Kivimäenpää *et al.*, 2003). However, during leaf senescence, the amount of starch in chloroplasts decreases (Keskitalo *et al.*, 2005) and the abundance of starch grains in the chloroplasts in autumn could indicate disturbance of photosynthate transport (Wulff *et al.*, 1996).

During senescence, the chloroplasts start to lose their regular shape and integrity of the thylakoid membranes (Biswal, 2005a; Evans *et al.*, 2010). Disarrangement of the thylakoid membrane is accompanied by formation of plastoglobuli in the chloroplast stroma. Plastoglobuli are small (45–60 nm) vesicles filled with various lipid and lipophilic compounds and play a role in lipid biosynthesis and storage (Austin *et al.*, 2006). During chloroplast senescence and oxidative stress the number and/or size of the plastoglobuli is increased and they tend to form clusters (Tevini & Steinmüller, 1985; Biswal, 2005a; Austin *et al.*, 2006). In addition, the amount of cytoplasmic lipid bodies tends to increase during leaf senescence (Wulff *et al.*, 1996).

1.5.2 Effects of ozone on plant cell ultrastructure

The effects of ozone on the ultrastructure of coniferous and deciduous trees have been studied extensively (Kivimäenpää, 2003 and references therein) but other plant groups have received much less attention. The ozone damage typically starts from the outer cell layers and in the vicinity of stomata, then gradually advances to the inner cell layers (Kivimäenpää, 2003). Although the direct effects of ozone or its breakdown products

are confined to the cell apoplast (Long & Naidu, 2002), the effects of chronic (i.e. long-term elevated background concentrations) ozone exposure are seen first in the chloroplasts (Sutinen *et al.*, 1990; Holopainen *et al.*, 1996). The most commonly reported effects on cell ultrastructure in ozone exposure studies include increased number of chloroplasts with electron dense (dark) and/or granulated stroma, increased number of irregular and spherical shaped chloroplasts (Pääkkönen *et al.*, 1995; Anttonen & Kärenlampi, 1996; Oksanen *et al.*, 2001), and decreased cross-section area or length of chloroplasts (Sutinen *et al.*, 1990; Kainulainen *et al.*, 2000; Rinnan & Holopainen, 2004). Dilation (swelling and curling) of thylakoids has been reported in some studies (Oksanen *et al.*, 2001) while in others the thylakoid retained its integrity (Holopainen *et al.*, 1996; Utriainen *et al.*, 2000). The amount of starch can be either decreased (Sutinen *et al.*, 1990; Oksanen *et al.*, 2001; Rinnan & Holopainen, 2004) or increased (Ranieri *et al.*, 2001). Moreover, various changes in the number and size of plastoglobuli have been reported (Miyake *et al.*, 1989; Pääkkönen *et al.*, 1995; Mikkelsen & Heide-Jørgensen, 1996; Rinnan & Holopainen, 2004).

In the cytoplasm, ozone has been reported to increase the amount of cytoplasmic lipid bodies (Pääkkönen *et al.*, 1995) and the number of peroxisomes (Morré *et al.*, 1990; Oksanen *et al.*, 2003). Furthermore, changes in the shape of mitochondria have also been reported (Kivimäenpää, 2003).

1.5.3 Effects of UV-B radiation on the plant cell ultrastructure

The effects of supplemental UV-B radiation on the cell structure have been discussed in relatively few articles and most of these studies have been conducted on algae or trees. However, it seems that chloroplasts are the primary site of UV-B induced changes in the plant cells (Hollósy, 2002). The UV-B induced changes in chloroplasts are very similar to those detected under ozone exposure. Supplemental UV-B is reported to reduce the chloroplast (Fagerberg & Bornman, 1997, 2005; Santos *et al.*, 2004) and starch (Valkama *et al.*, 2003; Santos *et al.*, 2004;

Fagerberg & Bornman, 1997, 2005) volume density, decrease the number and size of the plastoglobuli (Zu *et al.*, 2010) and increase the number of chloroplasts with electron dense stroma (Wulff *et al.*, 1999). Dilation of thylakoid membranes has been reported in several vascular plant species (Brandle *et al.*, 1977; He *et al.*, 1994; Bornman *et al.*, 1983; Hollósy, 2002; Kostina *et al.*, 2001). In addition, the amount of the thylakoid membranes and the ratio between appressed and non-appressed thylakoids can be altered (Yu & Björn, 1999; Fagerberg & Bornman, 1997).

In the cytoplasm, supplemental UV-B is reported to induce formation of abnormal membrane whorls (Kostina *et al.*, 2001; Valkama *et al.*, 2003), and increase the number of cytoplasmic lipid bodies (Kostina *et al.*, 2001; Wulff *et al.*, 1999). The volume density of mitochondria is either increased (Heijari *et al.*, 2006) or decreased (Fagerberg & Bornman, 2005).

1.6 PLANT PHOTOSYNTHESIS AND ABOVE-GROUND BIOMASS

1.6.1 Effects of tropospheric ozone on plant photosynthesis and biomass production

Ozone has been reported to decrease net photosynthesis in a variety of plant groups. The effects of ozone on trees and crop plants are particularly well documented (e. g. Novak *et al.*, 2005; Felzer *et al.*, 2007; Wittig *et al.*, 2007; Biswas, 2008). In natural vegetation, the negative effect on photosynthesis processes has been reported on both vascular plants (Reiling & Davison, 1994; Francini *et al.*, 2007; Hayes *et al.*, 2009) and bryophytes (Potter *et al.*, 1996). The primary cause of the decreased CO_2 assimilation under ozone exposure seems to be decreased concentration and/or activity of Rubisco (Pell *et al.*, 1997; Goumenaki *et al.*, 2010), although decreased photochemical efficiency of PSII has also been reported (Nussbaum *et al.*, 2001). The decrease of chlorophyll concentration, however, is considered to be a secondary response induced by the decreased carboxylation capacity rather than a direct effect of ozone exposure (Anderson *et al.*, 2003). The reduction in photosynthesis and the consequent

increase in plant internal CO_2 concentrations induces stomatal closure (Long & Naidu, 2002; Paoletti & Grulke, 2005) but prolonged ozone exposure can also directly damage the guard cells causing the stomata to become sluggish in their response to changes in environmental conditions (McAinsh *et al.*, 2002; Paoletti & Grulke, 2010). In both cases, the efficiency of the carbon binding processes can be decreased (Guidi *et al.*, 2002; Paoletti & Grulke, 2005).

Ozone often causes premature senescence (Bergman *et al.*, 1999; Franzaring *et al.*, 2000; Hayes *et al.*, 2006, 2010; Williamson *et al.*, 2010) and decreases biomass (above-ground or total) production (Morgan *et al.*, 2003; Rämö *et al.*, 2006; Hayes *et al.*, 2006, 2010). However, no effect (Nikula *et al.*, 2009) or even increased biomass (Pleijel & Danielson, 1997; Franzaring *et al.*, 2000) have also been reported. In their review of field layer vascular plant species, Timonen *et al.*, (2004) reported ozone induced growth reductions in 31% of the 55 studied species. However, four of these species showed initial growth stimulation under low ozone supplementation (40-45 ppb compared to the control concentration of 12-15 ppb). Ozone also causes a specific visible injury in plant leaves which has sometimes been used as an indicator of ozone sensitivity of plant species. However, the appearance of visible injuries correlates poorly with a decrease in biomass or reproductive success (Davison & Barnes, 1998).

1.6.2 Effects of UV-B on plant photosynthesis and biomass production

The effects of UV-B on various vascular plant species and the mechanisms behind these effects have been studied extensively under laboratory, growth chamber, green house and field conditions (Searles *et al.*, 2001a; Hollósy, 2002). Growth chamber studies have shown that UV-B has the potential to reduce photosynthesis and biomass accumulation of plants, stimulate the production of UV-B absorbing compounds, cause significant DNA damage, induce various morphological changes and affect the allocation of the photosynthesis products (Hollósy, 2002).

The experimental design can greatly affect the occurrence of UV-B effects. The ratios between the UV-B radiation, photosynthetically active radiation (PAR) and UV-A radiation is one of the most important factors in the experimental design because DNA repair processes require sufficient amounts of blue light and UV-A to function properly (Krizek, 2004). Therefore, the UV-B effects tend to be more pronounced in indoor experiments, in which the irradiation spectrum is often over-represented by UV-B, than in outdoor experiments with more intense UV-A and PAR (Krizek, 2004). While the experiments in strictly controlled growth chamber conditions are needed when the exact mechanisms of the UV-B induced effects are to be studied, outdoor experiments give a more realistic image of the extent of plant responses to increased UV-B radiation under natural conditions.

In outdoor experiments, plant photosynthesis is seldom affected and the direct effects of UV-B radiation are often limited to stimulation of UV-B absorbing compound synthesis and DNA damage repair processes (Searles et al., 2001a; Rozema et al., 2005; Newsham & Robinson, 2009). However, stimulation of the protection and repair processes can affect gas exchange and growth indirectly. Synthesis of the UV-B absorbing pigments and repair of the DNA damage can increase the maintenance respiration of the plants (Gwynn-Jones, 2001). Furthermore, allocation of the plant's resources to the pigment biosynthesis and the repair processes reduce the resources available to growth and reproduction (Newsham & Robinson, 2009). Thus, UV-B radiation may decrease the plant growth rate or above-ground biomass even if the photosynthesis process itself is not impaired (Xiong & Day, 2001; Newsham & Robinson, 2009).

Fewer UV-B studies have been conducted on bryophytes than on vascular plants (Boelen et al., 2006). Despite their comparatively simple leaf structure, and lack of protective cuticle, bryophytes are surprisingly well adapted to UV-B radiation and respond to it mostly in the same way as vascular plants (Gehrke, 1998, 1999; Newshan & Robinson, 2009).

However, the production of methanol-extractable UV-B absorbing compounds seems to be less responsive in bryophytes than in vascular plants (Boelen *et al.*, 2006; Martínez-Abaigar *et al.*, 2009). Gehrke (1999) even reported a decrease in UV-B absorbing compounds under supplemental UV-B in *Polytrichum commune*. The UV-B effects on growth and morphology of mosses have been variable (Johanson *et al.*, 1995; Boelen *et al.*, 2006; Lappalainen *et al.*, 2008). In *Sphagnum fuscum*, supplemental UV-B radiation increased net photosynthesis and decreased dark respiration (Gehrke, 1998). Branching, length growth, leaf density and biomass of individual shoots can be altered even if the biomass per area remains unaffected (Gehrke, 1998, 1999; Searles *et al.*, 2002; Lud *et al.*, 2002).

1.7 BELOW-GROUND ALLOCATION AND SOIL RESPIRATION

1.7.1 Effect of ozone on below-ground processes and soil respiration

Although ozone is highly hazardous to soil microbes and could also affect the soil quality by reacting with the carbon compounds in soil particles (Jones *et al.*, 2009), its direct effects are most likely limited to the topmost soil layer (Blum & Tingey, 1977). However, ozone can directly affect the microbes on the litter and soil surfaces and have a substantial indirect effect on soil processes through changes in litter quality and photosynthate allocation (Kim *et al.*, 1998; Andersen, 2003; Williamson *et al.*, 2010).

Several studies have reported decreased biomass allocation below-ground in ozone exposed plants (e.g. Franzaring *et al.*, 2000; Power & Ashmore, 2002; Andersen, 2003) although opposite effects (Franzaring *et al.*, 2000; Yamaji *et al.*, 2003) or no effects (Yoshida *et al.*, 2001; Andersen *et al.*, 2010) have also been reported. Plant mediated effects of ozone on soil microbial community and soil respiration are dependent on the used ozone concentration (Scagel & Andersen, 1997), plant species (Manninen *et al.*, 2010; Phillips *et al.*, 2002) and other stress

factors, such as drought (Nikolova *et al*., 2010). Decreased bulk soil microbial biomass has been reported in *Lathyrus pratensis* monoculture (Manninen *et al*., 2010) and in meadow mesocosms (Kanerva *et al*., 2008) but not in *Agrostis capillaris* monoculture (Manninen *et al*., 2010). In a study with pot-grown *Pinus ponderosa* seedlings, the active soil fungi biomass increased under low supplemental ozone, but decreased under high ozone concentration (Scagel & Andersen, 1997). In addition, the below-ground responses are not necessarily consistent with the ozone effects on photosynthesis or biomass production. For example, in a three year experiment with silver birch (*Betula pendula*), ozone exposure had a cumulative stimulating effect on soil respiration (Kasurinen *et al*., 2004) but no significant effect on the CO_2 assimilation of the leaves (Riikonen *et al*., 2005). In cotton (*Gossypium barbadense*) and melon (*Cucumis melo*), ozone decreased the CO_2 assimilation rate but increased the root respiration rate (Grantz *et al*., 2003) and Matyssek *et al*., (2010) reported similar effects in beech (*Fagus sylvatica*).

1.7.2 Effects of UV-B on below-ground processes and soil respiration

As UV-B radiation penetrates only a few millimetres into the peat layer (Searles *et al*., 2001b), its direct effect on soil respiration and the microbial community is limited. In xeric ecosystems, where the microbial activity on the soil surface is restricted by lack of water, UV-B radiation can directly increase the litter decomposition rate in the topmost soil layers by accelerating the photodegradation of lignin (Rozema *et al*., 1997; Smith *et al*., 2010). However, under more moist conditions, the negative effect of UV-B radiation on the decomposer community is greater than the effect of photodegradation leading to a decreased decomposition rate (Gehrke *et al*., 1995; Moody *et al*., 2001; Pancotto *et al*., 2003). In addition, UV-B radiation can have substantial and diverse indirect effects on soil processes through altered plant growth and chemistry. The UV-B induced changes in the chemical composition and physical properties during plant growth (Rozema *et al*., 1997; Cybulski *et al*., 2000) can

decrease the decomposability of plant litter (Gehrke *et al.*, 1995; Pancotto *et al.*, 2005), thus affecting the ecosystem respiration rate and causing changes in soil microbial community.

UV-B radiation can affect the allocation of photosynthesis products and thus cause changes in root biomass, turnover (Zaller *et al.*, 2002; Rinnan *et al.*, 2005, 2006) and root exudation (Avery *et al.*, 2003; Rinnan *et al.*, 2006). Changes in the availability of decomposable root material and in root exudation can in turn affect the activity, biomass and/ or composition of the soil microbial community (Johnson *et al.*, 2002, 2003; Rinnan *et al.*, 2005, 2008). UV attenuation studies demonstrate that the ambient solar UV-B radiation both in the Arctic and Antarctic can decrease the root growth (Zaller *et al.*, 2002, root length; Rinnan *et al.*, 2005 biomass) and root exudation thus causing changes in the microbial community in the rhizosphere (Avery *et al.*, 2003). Decreased root exudation has also been reported in an UV-B supplementation study with mire microcosms (Rinnan *et al.*, 2006). However, the effects of UV-B radiation on below-ground processes are even more variable than those on above-ground and are easily affected by other stress factors (Avery *et al.*, 2004; Andersen, 2003).

1.8 ECOSYSTEM CO_2 EXCHANGE

The effects of supplemental UV-B or ozone on CO_2 exchange of natural ecosystems has only been measured in a few studies. However, as reviewed in sections 1.6 and 1.7, both of these stressors can affect several plant and soil processes that contribute to the ecosystem carbon balance. Decreased above-ground biomass and the possible decrease in photosynthesis would lead to decreased ecosystem CO_2 uptake. The altered allocation below-ground could cause changes in soil respiration but could also affect the sequestration of plant material into the deeper soil layers. However, the effects of both UV-B radiation and tropospheric ozone seem to be very species-specific and dependent on other environmental factors. Therefore,

extrapolating long-term ecosystem level effects on the basis of single species responses is susceptible to errors.

In studies with peatland microcosms, 30% UV-B$_{CIE}$ supplementation (weighted with the erythemal action spectrum) decreased gross photosynthesis and net CO_2 exchange (Niemi *et al.*, 2002a) or increased the dark respiration rate (Rinnan *et al.*, 2003). Elevated ozone concentrations increased dark respiration rates both in peatland (Niemi *et al.*, 2002b; Rinnan *et al.*, 2003) and meadow microcosms (Kanerva *et al.*, 2007). However, in peatland ecosystems the effect was only transient (Niemi *et al.*, 2002b; Rinnan *et al.*, 2003) whereas in the meadow ecosystem the effect was not detected until the second and third exposure year (Kanerva *et al.*, 2007). In addition, several studies have predicted significant decreases in the ecosystem carbon sink due to increased tropospheric ozone (Feltzer *et al.*, 2005; Sitch *et al.*, 2007; Royal Society, 2008).

1.9 OBJECTIVES OF THE RESEARCH AND OUTLINE OF EXPERIMENTS

The main purpose of this thesis was to assess the future effects of a) increasing tropospheric ozone concentration b) increasing UV-B radiation level (stratospheric ozone depletion) on the CO_2 exchange of boreal mire ecosystems. In addition, responses of plant photosynthesis related factors to these stressors were studied in order to define the mechanisms behind possible ecosystem level changes. As the aim was to assess the probability and magnitude of the effects in natural ecosystems, the experiments were conducted under as natural conditions as was practically possible. The ozone exposure was conducted in a free-air exposure facility with fen microcosms (articles I and II). The UV-B supplementation study was conducted on a natural flark fen with a modulated UV-B exposure facility (articles III and IV). Since both of these stressors have a wide variety of indirect effects on decomposition and soil respiration that can take several years to become detectable at the ecosystem scale,

the exposures were continued for four (O_3) or three (UV-B) years. The study hypotheses and the methods used are summarized in Table 1.

Table 1. *Summary of the tested hypotheses and methods used.*

Hypotheses tested	Method	Chapter
Ozone induces changes in the fine structure and volume density of plant cell organelles, especially in the chloroplasts	• Analysis of transmission electron microscopy (TEM) sections	I
Ozone exposure decreases the photosynthetic efficiency of mire plants	• Measurement of light saturated CO_2 assimilation rate and the dark respiration rate using the dynamic chamber method • Measurement of the photochemical efficiency of PSII (F_v/F_m) with chlorophyll fluorescence measurements	II
Ozone exposure has a cumulative negative effect on the ecosystem CO_2 sink by decreasing P_G and increasing R_{TOT}	• Measurement of CO_2 exchange with the closed chamber method over four growing seasons using transparent and opaque chambers.	II
UV-B induces moderate changes in the fine structure and volume density of plant cell organelles, especially in the chloroplasts	• Analysis of TEM sections	III
Supplemental UV-B decreases the photosynthetic efficiency of *Eriophorum russeolum*.	• Measurement of light saturated CO_2 assimilation rate and the dark respiration rate using the dynamic chamber method • Measurement of the photochemical efficiency of PSII (F_v/F_m) with chlorophyll fluorescence measurements	III
Supplemental UV-B radiation decreases the plant growth rate	• Growth measurements in the field	III
Supplemental UV-B has a cumulative negative effect on the ecosystem CO_2 sink by decreasing P_G and increasing R_{TOT}	• Measurement of CO_2 exchange over three years with the closed chamber method using transparent and opaque chambers and snow gradient method.	IV

2 Discussion

2.1 OPEN FIELD OZONE EXPOSURE

The effects of increased ozone concentration on the photosynthetic properties of two fen plants, tussock cottongrass (*Eriophorum vaginatum* L.) and a moss *Sphagnum papillosum* Lindb., and on the CO_2 exchange of the fen microcosms were studied during four consecutive growing seasons, 2003-2006. The fen microcosms with intact vegetation and peat layers were cored at the end of May 2003 and installed into the ground of the experimental fields soon after the coring in order to maintain natural peat temperatures. The microcosms were exposed to either ambient ozone concentrations or to elevated ozone concentrations from mid-May to early October. The realized ozone elevation during the growing seasons (2003-2006) was 1.7-1.9 times the ambient ozone concentrations at the ground surface level. The ambient ozone concentrations on the site tended to be highest in early summer, especially in 2003 and 2005 (Häikiö *et al.*, 2009; article I). A detailed description of the original fen can be found in Saarnio *et al.*, (1997) and the description of the ozone exposure facility is given in article I and in Mörsky *et al.* (2008).

2.1.1 Effects of elevated ozone concentration on photosynthetic machinery

The ultrastructure of the mesophyll cells of the *Eriophorum vaginatum* leaves and chlorophyllose cells of *Sphagnum papillosum* leaves was studied with transmission electron microscopy (TEM) in 2003-2005 (article I). The photochemical efficiency of PSII in a dark adapted state (F_v/F_m) of fully expanded *E. vaginatum* leaves was studied with chlorophyll fluorescence measurements during four growing seasons (2003-2006) and the light saturated net CO_2 assimilation was measured

with the dynamic-chamber method in August 2004 and in July 2005 (article II).

In an earlier growth chamber study with microcosms collected from the same fen, ozone caused a variety of changes in the ultrastructure of both *E. vaginatum* and *S. papillosum* (Rinnan & Holopainen, 2004). Although the effects were clearest in plants exposed to 100ppb ozone concentration (accumulated ozone exposure over a threshold of 40 ppb, AOT_{40} = 12.4 ppm h), some changes were already detected at 50ppb concentration (AOT_{40} = 7.1 ppm h). In our study, the AOT_{40} values in the ozone treatment were substantially higher (20.8-35.8 ppm h in 2003-2006) than in the growth chamber study due to longer exposure periods, although the average of the daily mean ozone concentrations was quite low (approximately 35 ppb in the ozone treatment). Nonetheless, the elevated ozone concentration had no significant effect on the ultrastructure of either of the studied species in the free air exposure (article I, tables 2 and 4) and only some seasonal changes were detected. The chloroplast area and the amount of starch in the *E. vaginatum* leaves decreased towards autumn. The slight decrease in grana stack thickness and increased number of plastoglobuli in late summer/autumn may indicate senescence related disintegration of the thylakoid membrane (Biswal, 2005a). Furthermore, the ultrastructure of *S. papillosum* was unaffected despite its apparent ozone sensitivity in the earlier microcosm studies (Rinnan & Holopainen, 2004) and the transient growth reductions in our study in 2005 (article I).

Supplemental ozone had variable effects on the F_v/F_m of the *E. vaginatum* leaves, indicating changes in the photochemical efficiency of PSII (article II). The F_v/F_m initially increased in the ozone treatment in August 2003 (week 31) but decreased in mid-July 2005 (week 28). The decrease in the F_v/F_m under elevated ozone concentrations in summer 2005 was mainly due to increased minimal fluorescence in the dark adapted state (F_0) indicating either impaired transfer of excitation energy to the reaction centres or damaged PSII reaction centre. The decrease in F_v/F_m was accompanied by changes in the growth rate and in

photosynthetical pigments (article I). The growth rate of *E. vaginatum* leaves was temporarily decreased in early June and the Chl-a/Chl-b ratio was increased in late June under the ozone treatment. Unlike the annual variation of the F_v/F_m response, the transient reduction of the relative growth rate of *E. vaginatum* recurred each spring, although the decrease was significant only in 2005 (article I). No effect on the rate of CO_2 assimilation of *E. vaginatum* was found during either of the measurement periods in August 2004 and July 2005 (article II). However, the timing of the CO_2 assimilation measurements was not best suited for detection of possible ozone responses since the ozone responses seemed to concentrate in early summer. Ozone uptake by plants is highest during vigorous growth when the stomata are open, which could explain the timing of the detected ozone responses. In addition, sunny weather (high PAR levels) during the spring and early summer in 2005 (article I, figure 1) could have amplified the effects of ozone (Guidi *et al*., 2000; Kivimäenpää *et al*., 2004).

2.1.2 Responses of ecosystem CO_2 exchange to elevated O_3 concentration

The instantaneous CO_2 exchange of the peatland microcosms was measured fortnightly (2003-2005) or once every three weeks (2006) with the closed chamber method during four growing seasons (article IV). At the beginning of the experiment (2003), the sedge leaf density (leaves/ m^2) was slightly lower in the ozone treatment than in the ambient control (Mörsky *et al*., 2008). Therefore, the leaf density was used as a covariate in the statistical analysis. However, the leaf density increased more in the ozone exposed microcosms than in the control microcosms and ended up being 18.5% higher in the ozone treatment in 2006.

Despite the increased F_v/F_m, the light saturated instantaneous gross photosynthesis (P_G) was decreased under elevated ozone concentrations during the first year (2003). However, unlike the recurrent but short-term growth rate reduction detected only in early summers, the negative effect on P_G amplified towards

autumn and disappeared during the second growing season (2004). The additional stress from coring of the microcosms could have caused the ecosystem to be more susceptible to ozone stress at the beginning of the experiment. However, in earlier microcosm studies, no such effect was found (Niemi *et al*., 2002b; Rinnan *et al*., 2003). High peak ozone concentrations in early summer 2003 (Häikiö *et al*., 2009) could also have been the reason for the decreased P_G.

In 2004 and 2005, no treatment effect on the ecosystem level gas exchange could be seen. However, in 2006, the rates of both P_G and total dark respiration (R_{TOT}) tended to be higher in the ozone treatment (article II). Despite the springtime reduction in the length growth of *E. vaginatum*, the biomass of individual leaves was probably not affected due to an increased cross-section area of the leaves (article I). Since the sedge leaf density also increased under ozone exposure, long-term ozone exposure did not affect the ecosystem gas exchange per unit of plant biomass but increased the amount of photosynthesizing biomass. The peat microbial biomass and organic acid concentrations in the peat pore water were higher under the ozone treatment at the end of the third growing season (2005) (Mörsky *et al*., 2008). Therefore, the increasing trend of R_{TOT} could be a result of increased microbial respiration, enhanced by the increased root exudation. An increase in the plant growth rate or biomass under moderately increased ozone concentrations (40 ppb) has been reported in some species (Timonen *et al*., 2004; Hayes *et al*., 2006). However, even in these cases, higher ozone concentrations (80 ppb) tend to decrease the growth rate (Timonen *et al*., 2004). In our study, the daily mean ozone concentrations averaged 35 ppb in the ozone treatment, but occasionally reached as high as 95.4 ppb. Since the AOT_{40} values were also considerably high, increased P_G was unexpected and demonstrates the importance of long-term studies on ecosystem level responses. In this case, the experiment could not be continued because the moss column started to grow out of the microcosms.

In other studies, the effects of ozone on ecosystem CO_2 exchange have been variable. In a growth chamber study with similar fen microcosms, elevated ozone concentrations increased ecosystem R_{TOT} and decreased the net ecosystem CO_2 exchange (NEE) (Rinnan *et al.*, 2003). However, in our study, NEE also increased due to increased P_G. In an open-top chamber study with *S. papillosum* and *E. vaginatum* dominated mire microcosms in the U.K, ozone did not affect R_{TOT} but decreased methane emissions (Toet *et al.*, 2011), which is in accordance with results from our experiment (Mörsky *et al.*, 2008). In contrast, long-term free air ozone exposure of sub-alpine grassland mesocosms decreased both R_{TOT} and P_G (Volk *et al.*, 2011). It has been suggested that among mire types, fens with a variety of vascular plant species may be more susceptible to changes in below-ground processes than *Sphagnum*-dominated acidic bogs because the above-ground changes are mediated into the deeper peat layers through the plant root system (Jones *et al.*, 2009).

2.2 NATURAL FEN ECOSYSTEM AND UV–B EXPOSURE

2.2.1 UV-B exposure

The effects of supplemental UV-B radiation on two mire plants species; red cottongrass *Eriophorum russeolum* Fr. ex Hartm. and a moss *Warnstorfia exannulata* (Schimp.) Loeske, and on the ecosystem level gas exchange was studied over a three year period (2003-2005). The UV-B exposure field was established on a mesotrophic flark fen in Sodankylä, northern Finland. The experimental facility consisted of 30 plots that were divided into three treatments: ambient control, UV-A control and UV-B treatment. Each treatment contained ten plots and the UV-B exposure commenced in June 2003. A detailed description of the experimental site and the exposure facility is given in article IV.

The target UV-B$_{CIE}$ supplementation was +46% (simulating 20% stratospheric ozone depletion) compared to the continuously measured ambient UV-B$_{CIE}$ level. However, due to technical problems, the actual UV-B$_{CIE}$ supplementation level

was much higher than intended during the first growing season (+63%) and considerably lower in 2005 (+21%) (articles III and IV). In 2004, when the overall ambient UV-B$_{CIE}$ dose was lowest, the supplementation was +37%.

2.2.2 The effects of supplemental UV-B on the ultrastructure of peatland plants

The dominant plants species on the fen, *E. russeolum* and *W. exannulata*, were sampled for ultrastructure analysis (article III). Only a few studies have discussed the effects of moderately increased UV-B radiation on the ultrastructure of vascular plants or bryophytes (chapter 1.5.3). In an earlier microcosm study, the leaf anatomy of a sedge species, *Eriophorum vaginatum,* from the same genus, was affected by supplemental UV-B (Niemi *et al.*, 2002a). However, in our study, the long-term UV-B exposure had no effect on the ultrastructure of either of the studied species, and only seasonal and annual changes were detected. In *E. russeolum*, the number of mitochondria stayed quite stable during the growing seasons and between years. However, the chloroplasts and starch volume densities varied greatly during the growing seasons. The chloroplast volume density decreased towards autumn as the vacuolar space increased. In addition, the starch volume density was lowest in late autumn and senescence related changes (Biswal, 2005a; Evans *et al.*, 2010) in chloroplast structure, such as dilated thylakoids and spherical chloroplasts became more common in autumn. Similar seasonal changes have been reported in several species (see chapter 1.5.3).

The studied moss, *W. exannulata*, was similarly unresponsive to supplemental UV-B (article III). The structure of the leaf cells was characterized by one or two chloroplasts with a couple of electron-dense (dark) plastoglobuli, and only a few other cell organelles visible in a cross section. Although the cell cross-section area of *W. exannulata* was only a fraction of that of *E. russeolum*, the cell walls were approximately the same thickness (average 0.53μm in *W. exannulata*, 0.61μm in *E. russeolum*) which might have protected the moss from the effects of UV-B

radiation. Overall, the cell structure was similar to that of the chlorophyllose cells of *Sphagnum* species (Rinnan & Holopainen, 2004). The chloroplasts contained very little or no starch, which could indicate a low photosynthetic efficiency. This was supported by the CO_2 exchange measurements conducted under laboratory conditions with moss layer cuttings (article III). It would seem that despite its simple leaf structure, *W. exannulata* was fairly well protected against UV-B radiation.

2.2.3 Responses of plant photosynthesis, growth and related properties to supplemental UV-B

The effects of supplemental UV-B radiation on plant specific gas exchange, chlorophyll fluorescence and the relative growth rate of *E. russeolum* was measured in 2004 and 2005 (article III). The maximum efficiency of PSII (F_v/F_m) was temporarily increased in June 2005 under supplemental UV-B radiation. This is surprising because excess light energy should have a negative effect on the efficiency of the photosystem and decreased F_v/F_m has been reported in some species (Heijari *et al.*, 2006; Albert *et al.*, 2010). However, no further UV-B effects on the F_v/F_m were detected.

The lack of UV-B response in the chloroplast structure of *E. russeolum* was accompanied with no changes in the plant specific CO_2 exchange. No effect on the light saturated net CO_2 assimilation rate or the dark respiration rate (R_d) of *E. russeolum* leaves were detected during either of the measurement years (2004 and 2005). Moreover, UV-B radiation had no effect on the light response of the CO_2 assimilation rate of *E. russeolum* but there were some seasonal changes in the shape of the light response curves (article III, figure 3). The CO_2 assimilation rate at low PAR levels (≤ 50 μmol m^{-2} s^{-1}) tended to increase towards autumn due to decreased dark respiration. Dark respiration decreased from -1.7 μmol CO_2 m^{-2} s^{-1} in July to -0.5 at the end of August in 2005 but the light saturated net CO_2 exchange stayed stable, indicating that the gross CO_2 assimilation rate decreased towards autumn approximately at the same rate as the dark respiration rate. Most of this decline could be explained by

decreasing energy demand for plant growth and reduced enzymatic activity due to the decreasing air temperature (article III, Fig. 1). Although the rate of light-saturated net photosynthesis decreased only slightly during the two months, the daily CO_2 uptake was significantly reduced by the decreasing daylight hours and solar angle. The CO_2 exchange of the moss layer was not affected by the supplemental UV-B. However, the light saturated net CO_2 uptake of the moss layer was very low (0.12 ± 0.03 mmol CO_2 m^{-2} h^{-1} = 1.44 ± 0.36 mg C m^{-2} h^{-1}) and thus the detection of possible UV-B effects would be very difficult under these conditions.

The overall lack of a UV-B effect on CO_2 assimilation was supported by the photosynthetical pigment analysis by Mörsky *et al.* (unpublished). The supplemental UV-B radiation did not have any significant effect on the concentrations of the carotenoids or chlorophylls in *E. russeolum* leaves (Mörsky *et al.*, unpublished). However, the concentration of cell wall bound UV-B absorbing compounds was transiently increased at the end of the first growing season (2003). This is in line with the current meta-analysis by Newsham and Robinson (2009), which suggests that in outdoor conditions, UV-B radiation rarely affects plant photosynthesis and the overall effects are likely to be limited to increased concentrations of UV-B absorbing compounds and possible indirect effects on plant growth. However, in our experiment, there were no significant UV-B effects on the relative growth rate (article III) or the rate of senescence (Mörsky *et al.*, unpublished) of *E. russeolum* leaves.

2.2.4 Seasonal evolution of the CO_2 exchange and the regulating factors

The instantaneous CO_2 exchange rates (NEE and R_{TOT}) of the fen ecosystem were measured with the closed chamber method during three growing seasons, 2003-2005 (article IV). The growing season CO_2 balance of the fen ecosystem was then estimated with nonlinear regression models and cumulative winter-time CO_2 efflux was extrapolated from snow-gradient measurements.

The water table level on the site and, subsequently, the CO_2 balance of the fen ecosystem were clearly affected by both the total amount of rainfall and by the timing of the rain. The range of water table level changes on the site during the snow free period (1 June-30 September) was ±10cm from the moss surface, so the soil respiration was usually strongly limited by lack of oxygen. If the water table level decreased below the peat surface, the respiration rate increased rapidly (article IV). The first year, 2003, was the driest of the three experimental years, with total precipitation between 1 May and 30 September close to its long-term average (273 mm vs. 263 mm) and the water table level decreased to approximately 8cm below the moss surface. During that growing season, even the wet flark surface of the fen was a net source of CO_2.

During the second and third year the total amount of precipitation was almost 100 mm higher than the long-term average (361 and 367 mm in 2004 and 2005, respectively). However, the CO_2 balance of the two growing seasons differed greatly. In 2004, the amount of precipitation was distributed quite evenly and the water table stayed high throughout the growing season. This led to low respiration rates and net CO_2 uptake of 28.5 ± 5.0 g CO_2-C m^{-2} during the snow free period, which is comparable to the values measured on a mesotrophic flark fen in northern Finland (Aurela *et al.*, 2001) and *Eriophorum vaginatum* fen in southern Finland (Riutta *et al.*, 2007).

In 2005, the early summer was dry and the water table level soon decreased below the peat surface. In conjunction with high temperatures this caused a high respiration peak in late July. The drawdown of the water table possibly caused the floating surface peat carpet to depress and to press out the gas bubbles stored in the lower peat column. This caused a short period of remarkably high CO_2 and methane release rates, the CO_2 efflux reaching as high as 396 mg CO_2-C m^{-2} h^{-1} in some plots. The emission peak lasted for only a few days but its effect on the seasonal CO_2 balance was profound. The modelled cumulative NEE in July 2005 was 0.15 ± 0.02 g CO_2 m^{-2} compared to 16.4 g CO_2-C m^{-2} in July 2004. However, the regression models used

give poor estimates for the gas exchange rates during these kinds of episodic peaks because the pressure changes in the peat layer were not measured or included into the models.

The cumulative wintertime CO_2 effluxes were only 1–3% of the respiration during the snow free period (1 June-30 September) in all treatments. A high water table and the consequent formation of an ice layer on the peat surface before snowfall are probably the main reasons for the relatively low wintertime CO_2 effluxes in the study site (cf. Alm *et al.*, 1999; Saarnio *et al.*, 2003, Leppälä *et al.*, 2011).

2.2.5 Effects of UV-B radiation on ecosystem level CO_2 exchange

The effects of supplemental UV-B radiation on CO_2 exchange of a mire ecosystem have only been studied two microcosm studies (Niemi *et al.*, 2002a; Rinnan *et al.*, 2003). These studies demonstrated that supplemental UV-B radiation can cause changes in the carbon gas exchange of northern mires. However, development of ecosystem level responses can take several years and therefore, a longer term study was needed. This study is the first multi-year study on the effects of supplemental UV-B radiation on the CO_2 exchange of a natural mire ecosystem.

Although the experimental plots were randomly placed on the flark surface where the vegetation was most homogeneous, the photosynthesizing leaf area (leaf area index, LAI) was slightly higher in the UV-B treatment plots from the start of the experiment (article IV). Because of this, both instantaneous P_G and R_{TOT} were higher in the UV-B plots. LAI also varied greatly between the years, but was not affected by supplemental UV-B or UV-A. Most of the photosynthesizing vascular plant area consisted of *E. russeolum* leaves and, therefore, the shoot density of *E. russeolum* was used as a covariate in the statistical analysis.

During the first two growing seasons (2003-2004), there was no significant UV-B effect on the instantaneous CO_2 exchange (article IV). In the third growing season (2005), the R_{TOT} rate was significantly lower in the UV-B treatment during the CO_2 emission peak, resulting in the higher light saturated NEE in

UV-B treatment. However, these changes were only significant if compared to the ambient control. Cloudy weather in autumn limited the measurement times of the light saturated CO_2 exchange and no comprehensive data on the evolution of the light saturated NEE and P_G in late August or September is available. However, the detected difference in instantaneous R_{TOT} disappeared by the end of August (Fig. 1) and no treatment effect could be seen in the winter CO_2 effluxes. Therefore, the role of the actual UV-B supplementation in decreased R_{TOT} is unclear. However, both UV-B and UV-A control treatments decreased bacterial growth rates in the surface (0-10cm) peat and altered the composition of the peat microbial community in 2005 (Rinnan *et al.*, 2008). In the deeper peat layers, bacterial growth was increased in the UV-A control treatment. In addition, UV-B exposure has repeatedly been shown to militate against soil microbes and decomposition of plant material (Johnson *et al.*, 2002; Duguay & Klironomos, 2000). During an abnormally dry summer in the fourth exposure year (2006), instantaneous NEE was transiently increased in both the UV-A control and UV-B treatments in comparison to the ambient control (Tiiva *et al.*, 2007). However, in 2008, the difference in the NEE between the treatments had disappeared once more (Faubert *et al.*, 2010).

When the modelled seasonal CO_2 balances (1 June–30 September) were compared, the cumulative NEE was higher in the UV-B treatment than that in the ambient control in 2005. The difference between the treatments in the CO_2 balance was greatest after the CO_2 emission peak in July (article IV figure 5). Although the instantaneous R_{TOT} (measured concurrently with the light-saturated NEE) was decreased under elevated UV-B during that period, the effect did not carry over to the seasonal CO_2 balance. However, it must be noted that the fit of the R_{TOT} models were poor during the CO_2 peak in mid-summer 2005 because most of the CO_2 emissions during that period were probably a result of bubbling-out of the CO_2 stored in the peat layer instead of direct soil respiration.
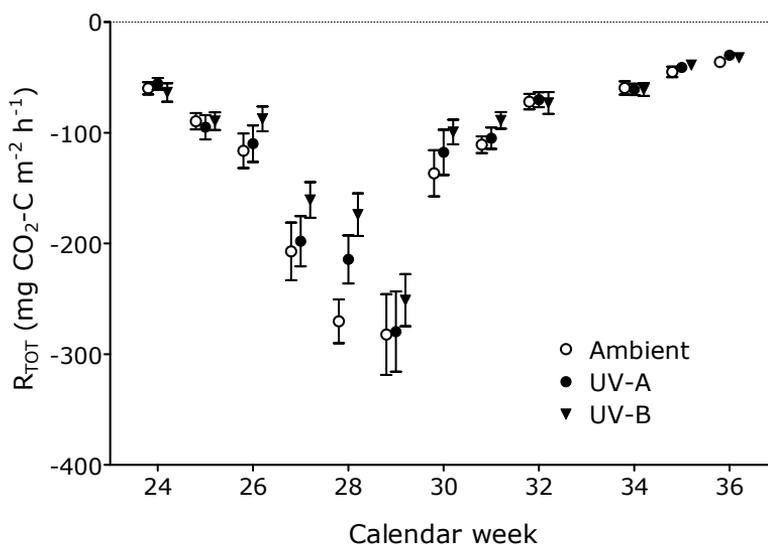
Figure 1. *The weekly mean (±SE) of ecosystem dark respiration (R_{TOT})*
rates in 2005.

2.3 CONCLUSIONS AND IMPLICATIONS

The effects of long-term ozone exposure on the studied mire plants and on the ecosystem level CO_2 exchange were minor (Table 2). Photosynthesis and growth related responses were transient and occurred mostly during or after high springtime ozone concentrations. No evidence of cumulative ozone effects or changes that could be related to acclimation to higher ozone concentrations was seen in the studied plant species. The ecosystem level CO_2 exchange was significantly affected only during the first growing season in the presence of additional physical stress (coring of the microcosms in 2003). As a more long-term effect, the elevated ozone concentrations slightly increased the sedge leaf density, thus causing an increase in both P_G and R_{TOT}. Although the increase was not statistically significant, it demonstrates the importance of long-term experiments. Since the negative effect of ozone on plant photosynthesis and growth have been demonstrated in a wide variety of species, it is unlikely that the now detected positive

42

effect on ecosystem P_G would be constant over the long term. Moreover, further studies are needed to determine the actual cause behind the increased plant biomass. On the basis of our results, it seems unlikely that the predicted increase in the background concentration of ozone would significantly decrease the net CO_2 uptake of northern fen ecosystem. Nevertheless, episodes of high ozone concentrations can cause transient reductions in photosynthetic efficiency and growth of the mire plants.

The results from the UV-B supplementation experiment show that the effects of long-term UV-B exposure on the mire ecosystem are very subtle. Supplemental UV-B had no significant effect on the ultrastructure, photosynthetic performance or growth of the studied fen plants; *Eriophorum russeolum* and *Warnstorfia exannulata* (Table 2). Even the highest UV-B$_{CIE}$ supplementation in 2003 (+63%) did not have any detectable effect on CO_2 exchange. Instead, a much lower supplementation level (+21%) in 2005 seemed to decrease the ecosystem level soil respiration rate during a sudden decrease in the water table. However, the overall high variability of the CO_2 exchange rates during such events causes additional uncertainty as to the actual causes of the detected difference between the treatments. On a fen with a high water table, even small differences in the water level can cause significant changes in the soil respiration. Therefore, the natural variations in the other environmental conditions easily mask the potential effects of the UV-B supplementation. Since the comparatively high UV-B radiation levels used in this study failed to induce any permanent changes in the plant growth or ecosystem level CO_2 exchange it is unlikely that the future levels of UV-B radiation would significantly affect the CO_2 balance of northern fens.

Table 2. Summary of the tested hypotheses and the obtained results.

Hypothesis tested	Acquired results	Chapter
Ozone induces changes in the fine structure and volume density of plant cell organelles, especially in the chloroplasts	• Ozone did not affect the ultrastructure of photosynthesizing cells *E. vaginatum* or *S. papillosum*	I
Ozone exposure decreases the photosynthetic efficiency of mire plants	• Ozone caused various transient effects on the F_v/F_m of *E. vaginatum* but had no permanent effect on the CO_2 assimilation.	II
Ozone exposure has a cumulative negative effect on the ecosystem CO_2 sink by decreasing P_G and increasing R_{TOT}	• Elevated ozone concentrations increased the sedge leaf density and tended to increase both R_{TOT} and NEE.	II
Supplemental UV-B induces moderate changes in the ultrastructure and volume density of plant cell organelles, especially in the chloroplasts	• Supplemental UV-B had no significant effect on the ultrastructure of *E. russeolum* or *W. exannulata* growing on a natural fen ecosystem.	III
Supplemental UV-B decreases the photosynthetic efficiency of *Eriophorum russeolum*.	• No significant effect on light saturated CO_2 assimilation or the dark respiration rate of *E. russeolum*. • Supplemental UV-B caused only a transient increase in the quantum efficiency of PSII (Fv/Fm) on the third exposure year.	III
Supplemental UV-B radiation decreases the plant growth rate	• No effect on the growth of *E. russeolum*.	III
Supplemental UV-B has a cumulative negative effect on the ecosystem CO_2 sink by decreasing P_G and increasing R_{TOT}	• No significant negative effect on ecosystem CO_2 uptake.	IV

References

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, New York, NY, USA.

Albert KR, Mikkelsen TN, Ro-Poulsen H, Michelsen A, Arndal MF, Brendahl L, Håkansson KB, Boesgaard K & Schmidt NM (2010) Improved UV-B screening capacity does not prevent negative effects of ambient UV irradiance on PSII performance in High Arctic plants. Results from a six year UV exclusion study. *Journal of Plant Physiology* 167: 1542–1849.

Albertsson P-Å (1995) The structure and function of the chloroplast photosynthetic membrane – a model for the domain organization. *Photosynthesis Research* 46: 141–149.

Alm J, Talanov A, Saarnio S, Silvola J, Ikkonen E, Aaltonen H, Nykänen H & Martikainen P J (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110: 423–431.

Alm J, Saarnio S, Nykänen H, Silvola J & Martikainen P J (1999) Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands. *Biogeochemistry* 44: 163–186.

Andersen C P (2003) Source-sink balance and carbon allocation below ground in plants exposed to ozone. *New Phytologist* 157: 213–228.

Andersen C P, Ritter W, Gregg J, Matyssek R & Gram T E E (2010) Below-ground carbon allocation in mature beech and spruce trees following long-term, experimentally enhanced O_3 exposure in Southern Germany. *Environmental Pollution* 158: 2604–2609.

Anderson P D, Palmer B, Houpis J L J, Smith M K & Pushnik J C (2003) Chloroplastic responses of ponderosa pine (*Pinus ponderosa*) seedlings to ozone exposure. *Environment International* 29: 407–413.

Anderson J M, Chow W S & De Las Rivas J (2008) Dynamic flexibility in the structure and function of photosystem II in higher plant thylakoid membranes: the grana enigma. *Photosynthesis Research* 98: 575–587.

Andersson B & Anderson J M (1980) Lateral heterogeneity in the distribution of chlorophyll-protein complexes of the thylakoid membranes of spinach chloroplasts, *Biochimica et Biophysica Acta (BBA) - Bioenergetics* 593: 427–440.

Anttonen S & Kärenlampi L (1996) Slightly elevated ozone exposure causes cell structural changes in needles and roots of Scots pine. *Trees* 10: 207–217.

Ashmore M R (2005) Assessing the future global impacts of ozone on vegetation. *Plant, Cell and Environment* 28: 949–964.

Aurela M, Laurila T & Tuovinen J P (2001) Seasonal CO_2 balances of a subarctic mire. *Journal of Geophysical Research* 106: 1623–1637.

Austin J R, Frost E, Vidi P-A, Kessler F & Staehelin L A (2006) Plastoglobules are lipoprotein subcompartments of the chloroplast that are permanently coupled to thylakoid membrane and contain biosynthetic enzymes. *The Plant Cell* 18: 1693–1703.

Avery L M, Smith R I L & West H M (2003) Response of rhizosphere microbial communities associated with Antarctic hairgrass (*Deschampsia antarctica*) to UV radiation. *Polar Biology* 26: 525–529.

Avery L M, Thorpe P C, Thompson K, Paul N D, Grime J P & West H M (2004) Physical disturbance of an upland grassland influences the impact of elevated UV-B radiation on metabolic profiles of below-ground micro-organisms. *Global Change Biology* 10: 1146–1154.

Bedford B L, Bouldin D R & Beliveau B D (1991) Net oxygen and carbon-dioxide balances in solution bathing roots of wetland plants. *Journal of Ecology* 79: 943–959.

Bergman E, Bender J & Weigel H-J (1999) Ozone threshold doses and exposure-response relationships for the development of ozone injury symptoms in wild plant species. *New Phytologist* 144: 423–435.

Biswal B (2005a) Formation and demolition of chloroplast during leaf ontogeny. *In*: Handbook of Photosynthesis edited by Pessarakli M. 2nd ed. CRC Press, Boca Raton, FL, USA. Pages 109–122.

Biswal B (2005b) Photosynthetic response of green plants to environmental stress: inhibition of photosynthesis and adaptational mechanisms. *In*: Handbook of Photosynthesis edited by Pessarakli M. 2nd ed. CRC Press, Boca Raton, FL, USA. Pages 739–749.

Biswas D K, Xu H, Li Y G, Sun J Z, Wang X Z, Han X G & Jiang G M (2008) Genotypic differences in leaf biochemical, physiological and growth responses to ozone in 20 winter wheat cultivars released over the past 60 years. *Global Change Biology* 14: 46–59.

Blum U & Tingey D T (1977) A study of the potential ways in which ozone could reduce root growth and modulation of soybean. *Atmospheric Environment* 11: 737–739.

Boelen P, de Boer M K, de Bakker N V J & Rozema J (2006) Outdoor studies on the effects of solar UV-B on bryophytes: overview and methodology. *Plant Ecology* 182: 137–152.

Bornman J F, Evert R F & Mierzwa R J (1983) The effect of UV-B and UV-C radiation on sugar beet leaves. *Protoplasma* 117: 7–16.

Brandle J R, Campbell W F, Sisson W B & Caldwell M M (1977) Net photosynthesis, electron transport capacity, and ultrastructure of *Pisum sativum* L. exposed to ultraviolet-B radiation. *Plant Physiology* 60: 165–169.

Bubier J L, Frolking S, Crill P M & Linder E (1999) Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research-Atmospheres* 104 Issue: D22 Pages: 27683–27692.

Chapin F S III, Matson P A & Mooney H (2002) Principles of terrestrial ecosystem ecology. Springer-Verlag New York, Inc, New York, USA.

Clymo R S (1983) Peat. In: Gore A J P (edit) *Ecosystems of the world 4A Mires: swamp, bog, fen and moor General studies.*

Elsevier scientific publishing company, Amsterdam, Netherlands. Pages 159–224.

Cybulski W J, Peterjohn W T & Sullivan J H (2000) The influence of elevated ultraviolet-B radiation (UV-B) on tissue quality and decomposition of loblolly pine (*Pinus taeda* L.) needles. *Environmental and Experimental Botany* 44: 231–241.

Davison A W & Barnes J D (1998) Effects of ozone on wild plants. *New Phytologist* 139: 135–151.

Denman K L, Brasseur G, Chidthaisong A, Ciais P, Cox P M, Dickinson R E, Hauglustaine D, Heinze C, Holland E, Jacob D, Lohmann U, Ramachandran S, da Silva Dias P L, Wofsy S C & Zhang X (2007) Couplings between changes in the climate system and biogeochemistry. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K B, Tignor M & Miller H L (eds) *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change.* Cambridge University Press, Cambridge, UK and New York, NY, USA.

Duguay K J & Klironomos J N (2000) Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprotrophic fungi. *Applied Soil Ecology* 14: 157–164.

Evans I M, Rus A M, Belanger E M, Kimoto M & Brusslan J A (2010) Dismantling of Arabidopsis thaliana mesophyll cell chloroplasts during natural leaf senescence. *Plant Biology* 12: 1–12.

Fagerberg W R & Bornman J F (1997) Ultraviolet-B radiation causes shade-type ultrastructural changes in *Brassica napus*. *Physiologia Plantarum* 101: 833–844.

Fagerberg W R & Bornman J F (2005) Modification of leaf cytology and anatomy in *Brassica napus* grown under above ambient levels of supplemental UV-B radiation. *Photochemical & Photobiological Sciences* 4: 275–279.

Farrar J, Hawes M, Jones D & Lindow S (2003) How roots control the flux of carbon to the rhizosphere. *Ecology* 84: 827–837.

Faubert P, Tiiva P, Rinnan Å, Räsänen J, Holopainen J K, Holopainen T, Kyrö E & Rinnan R (2010) Non-methane biogenic volatile organic compound emissions from a subarctic peatland under enhanced UV-B radiation. *Ecosystems* 13: 860–873.

Felzer B, Reilly J, Melillo J, Kicklighter D, Sarofim M, Wang C, Prinn R & Zhuang Q (2005) Future effects of ozone on carbon sequestration and climate change policy using a global biogeochemical model. *Climatic Change* 73: 345–373.

Felzer B S, Cronin T, Reilly J M, Melillo J M, Wang X (2007) Impacts of ozone on trees and crops. *Comptes Rendus Geosciences* 339: 784–798.

Foyer C H & Noctor G (2005) Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. *Plant, Cell and Environment* 28: 1056–1071.

Francini A, Nali C, Picchi V & Lorenzini G (2007) Metabolic changes in white clover clones exposed to ozone. *Environmental and Experimental Botany* 60: 11–19.

Franzaring J, Tonneijck A E G, Kooijman A W N & Dueck Th A (2000) Growth responses to ozone in plant species from wetlands. *Environmental and Experimental Botany* 44: 39–48.

Frolking S E, Bubier J L, Moore T R, Ball T, Bellisario L M, Bhardwaj A, Carroll P, Crill P M, Lafleur P M, McCaughey J H, Roulet N T, Suyker A E, Verma S B, Waddington J M & Whiting G J (1998) Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Global Biogeochemical Cycles* 12: 115–126.

Gehrke C, Johanson U, Callaghan T V, Chandwick D & Robinson C H (1995) The impact of enhanced ultraviolet-B radiation on litter quality and decomposition processes in *Vaccinium* leaves from the sub-arctic. *Oikos* 72: 213–222.

Gehrke C (1998) Effects of enhanced UV-B radiation on production-related properties of a *Sphagnum fuscum* dominated subarctic bog. *Functional Ecology* 12: 940–947.

Gehrke C (1999) Impacts of enhanced ultraviolet-B radiation on mosses in a subarctic heath ecosystem. *Ecology* 80: 1844–1851.

Gorham E (1991) Northern peatlands; role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1: 182–195.

Goumenaki E, Taybi T, Borland A & Barnes J (2010) Mechanisms underlying the impacts of ozone on photosynthetic performance. *Environmental and Experimental Botany* 69: 259–266.

Grantz D A, Silva V, Toyota M & Ott N (2003) Ozone increases root respiration but decreases leaf CO_2 assimilation in cotton and melon. *Journal of Experimental Botany* 54: 2375–2384.

Guidi L, Tonini M & Soldatini G F (2000) Effects of high light and ozone fumigation on photosynthesis in *Phaseolus vulgaris*. *Plant Physiology and Biochemistry* 38: 717–725.

Guidi L, Degl'Innocenti E & Soldatini G F (2002) Assimilation of CO_2, enzyme activation and photosynthetic electron transport in bean leaves, as affected by high light and ozone. *New Phytologist* 156: 377–388.

Gwynn-Jones D (2001) Short-term impacts of enhanced UV-B radiation on photo-assimilate allocation and metabolism: a possible interpretation for time-dependent inhibition of growth. *Plant Ecology* 154: 67–73.

Hayes F, Mills G, Williams P, Harmens H & Büker P (2006) Impacts of summer ozone exposure on the growth and overwintering of UK upland vegetation. *Atmospheric Environment* 40: 4088–4097.

Hayes F, Mills G & Ashmore M (2009) Effects of ozone on inter- and intra-species competition and photosynthesis in mesocosms of *Lolium perenne* and *Trifolium repens*. *Environmental Pollution* 157: 208–214.

Hayes F, Mills G, Jones L & Ashmore M (2010) Does a simulated upland grassland community respond to increasing background, peak or accumulated exposure of ozone? *Atmospheric Environment* 44: 4155–4164.

He J, Huang L K & Whitecross M I (1994) Chloroplast ultrastructure change in *Pisum sativum* associated with supplementary ultraviolet (UV-B) radiation. *Plant, Cell and Environment* 17: 771–775

Heath R L (2008) Modification of the biochemical pathways of plants induced by ozone: What are the varied routes to change? *Environmental Pollution* 155: 453-463.

Heijari J, Kivimäenpää M, Hartikainen H, Julkunen-Tiitto R & Wulff A (2006) Responses of strawberry (*Fragaria×ananassa*) to supplemental UV-B radiation and selenium under field conditions. *Plant and Soil* 282: 27–39.

Hollósy F (2002) Effects of ultraviolet radiation on plant cells. *Micron* 33: 179–197.

Holopainen T, Anttonen S, Palomäki V, Kainulainen P & Holopainen J K (1996) Needle ultrastructure and starch content in Scots pine and Norway spruce after ozone fumigation. *Canadian Journal of Botany* 74: 67–76.

Hudák J, Gálová E & Zemanová L (2005) Plastid morphogenesis. In: Pessarakli M (edit) *Handbook of Photosynthesis*, 2nd ed. CRC Press, Boca Ratonm, FL, USA. Pages 221–245.

Häikiö E, Makkonen M, Julkunen-Tiitto R, Sitte J, Freiwald V, Silfver T, Pandey V, Beuker E, Holopainen T & Oksanen E (2009) Performance and secondary chemistry of two hybrid aspen (*Populus tremula* L. x *Populus tremuloides* Michx.) clones in long-term elevated Ozone exposure. Journal of Chemical Ecology, 35: 664–678.

Johanson U, Gehrke C, Björn L O, Callaghan T V & Sonesson L (1995) The effects of enhanced UV-B radiation on a subarctic heath ecosystem. *Ambio* 24: 106–111.

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 CO_2. *Nature* 416: 82–83.

Johnson D, Campbell C D, Lee J A, Callaghan T V & Gwynn-Jones D (2003) UV-B radiation and soil microbial communities. *Nature* 423: 137–138.

Jones TG, Freeman C, Lloyd A, Mills G (2009) Impacts of elevated atmospheric ozone on peatland below-ground DOC characteristics. *Ecological engineering* 35: 971–977.

Joosten H (2009) *The Global Peatland CO_2 Picture: Peatland status and emissions in all countries of the world*, draft. Wetlands International and Greifswald University, Ede, Netherlands.

Kainulainen P, Utriainen J, Holopainen J K, Oksanen J & Holopainen T (2000) Influence of elevated ozone and limited nitrogen availability on conifer seedlings in an open-air fumigation system: effects on growth, nutrient content, mycorrhiza, needle ultrastructure, starch and secondary compounds. *Global Change Biology* 6: 345–355.

Kanerva T, Regina K, Rämö K, Ojanperä K & Manninen S (2007) Fluxes of N_2O, CH_4 and CO_2 in a meadow ecosystem exposed to elevated ozone and carbon dioxide for three years. *Environmental Pollution* 145: 818–828.

Kanerva T, Palojärvi A, Rämö K & Manninen S (2008) Changes in soil microbial community structure under elevated tropospheric O_3 and CO_2. *Soil Biology & Biochemistry* 40: 2502–2510.

Kangasjärvi J, Jaspers P & Kollist H (2005) Signalling and cell death in ozone-exposed plants. *Plant, Cell and Environment* 28: 1021–1036.

Kanofsky J R & Sima P D (1995) Singlet oxygen generation from the reaction of ozone with plant leaves. *The Journal of Biological Chemistry* 270: 7850–7852.

Kasurinen A, Kokko-Gonzales P, Riikonen J, Vapaavuori E & Holopainen T (2004) Soil CO_2 efflux of two silver birch clones exposed to elevated CO_2 and O_3 levels during three growing seasons. *Global Change Biology* 10: 1654–1665.

Keskitalo J, Berquist G, Gardeström P & Jansson S (2005) A cellular timetable of autumn senescence. *Plant Physiology* 139: 1635-1648.

Kim J S, Chappelka A H & Miller-Goodman M S (1998) Decomposition of blackberry and broomsedge bluestem as influenced by ozone. *Journal of Environmental Quality* 27: 953–960.

Kivimäenpää M, Sutinen S, Medin E-L, Karlsson P E & Sellden G (2001) Diurnal changes in microscopic structures of mesophyll cells of Norway spruce, *Picea abies* (L.) Karst., and the effects of ozone and drought. *Annals of Botany* 88: 119–130.

Kivimäenpää M (2003) The cell and tissue structures of norway spruce and Scots pine needles as tools for the diagnosis of ozone impact. Kuopio University Publications C. Natural and Environmental Sciences 157. Kuopio, Finland.

Kivimäenpää M, Sutinen S, Karlsson P E & Selldén G (2003) Cell structural changes in the needles of Norway spruce exposed to long-term ozone and drought. *Annals of Botany* 92: 779-793.

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. *Environmental Pollution* 127: 441–453.

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.

Krizek D T (2004) Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation. *Photochemistry and Photobiology* 79: 307–315.

Laisk A, Kull O & Moldau H (1989) Ozone concentration in leaf intercellular air spaces is close to zero. *Plant Physiology* 90: 1163-1167.

Lappalainen N M, Huttunen S & Suokanerva H (2008) Acclimation of a pleurocarpous moss *Pleurozium schreberi* (Britt.) Mitt. to enhanced ultraviolet radiation in situ. *Global Change Biology* 14: 321–333.

Laurila T, Jonson J E, Langner J, Sundet J, Tuovinen J-P, Bergström R, Foltescu V, Tarvainen V & Isaksen I S A

(2004a). *Ozone exposure scenarios in the Nordic countries during the 21st century*. EMEP/MSC-W Technical Report 2/2004. Norwegian Meteorological Institute, Oslo, Norway.

Laurila T, Tuovinen J P, Tarvainen V & Simpson D (2004b) Trends and scenarios of ground-level ozone concentrations in Finland. *Boreal Environment Research* 9: 167–184.

Leppälä M, Laine A M & Tuittila E-S (2011) Winter carbon losses from a boreal mire succession sequence follow summertime patterns in carbon dynamics. *Suo* 62: 1–11.

Long SP & Naidu S L (2002) Effects of oxidants at the biochemical, cell and physiological levels, with particular reference to ozone. In: Bell J N B & Treshow M (eds) *Air pollution and plant life*. John Wiley & Sons, Ltd, Chichester, UK. Pages 69–88.

Lud D, Moerdijk T C W, van de Poll W H, Buma A G J & Huiskes A H L (2002) DNA damage and photosynthesis in Antarctic and Arctic *Sanionia uncinata* (Hedw.) Loeske under ambient and enhanced levels of UV-B radiation. *Plant, Cell and Environment* 25: 1579–1589.

Mackerness S A-H (2000) Plant responses to ultraviolet-B (UV-B: 280–320 nm) stress: What are the key regulators? *Plant Growth Regulation* 32: 27–39.

Manney G L, Santee M L, Rex M, Livesey N J, Pitts M C, Veefkind P, Nash E R, Wohltmann I, Lehmann R, Froidevaux L, Poole L R, Schoeberl M R, Haffner D P, Davies J, Dorokhov V, Gernandt H, Johnson B, Kivi R, Kyrö E, Larsen N, Levelt P F, Makshtas A, McElroy C T, Nakajima H, Parrondo M C, Tarasick D W, von der Gathen P, Walker K A & Zinoviev N S (2011) Unprecedented Arctic ozone loss in 2011. *Nature* 478: 469-475.

Manninen S, Aaltonen H, Kanerva T, Rämö T & Palojärvi A (2010) Plant and soil microbial biomasses in *Agrostis capillaris* and *Lathyrus pratensis* monocultures exposed to elevated O_3 and CO_2 for three growing seasons. *Soil Biology & Biochemistry* 42: 1967–1975.

Martínez-Abaigar J, Otero S, Tomas R & Núñez-Olivera E (2009) Effects of enhanced ultraviolet radiation on six aquatic bryophytes. *Cryptogamie Bryologie* 30: 157–175.

Matyssek R, Wieser G, Ceulemans R, Rennenberg H, Pretzsch H, Haberer K, Löw M, Nunn A J, Werner H, Wipfler P, Oßwald W, Nikolova P, Hanke D E, Kraigher H, Tausz M, Bahnweg G, Kitao M, Dieler J, Sandermann H, Herbinger K, Grebenc T, Blumenröther M, Deckmync G, Grams T E E, Heerdt C, Leuchner M, Fabiane P & Häberle K-H, (2010) Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*) - resume from the free-air fumigation study at Kranzberg Forest. *Environmental Pollution* 158: 2527–2532.

McAinsh M R, Evans N H, Montgomery L T & North K A (2002) Calcium signalling in stomatal responses to pollutants. *New Phytologist* 153: 441-447.

McKinley 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*. Elsevier Science Publishers, Amsterdam, Netherlands. Pages 83–87.

Mikkelsen T N & Heide-Jørgensen H S (1996) Acceleration of leaf senescence in *Fagus sylvatica* L. by low levels of tropospheric ozone demonstrated by leaf colour, chlorophyll fluorescence and chloroplast ultrastructure. *Trees* 10: 145–156.

Miyake H, Matsumura H, Fujinuma Y & Totsuka T (1989) Effects of low concentrations of ozone on the fine structure of radish leaves. *New Phytologist* 111: 187–195.

Moody S A, Paul N D, Björn L O, Callaghan T V, Lee J A, Manetas Y, Rozema J, Gwynn-Jones D, Johanson U, Kyparissis A & Oudejans M C (2001) The direct effects of UV-B radiation on Betula pubescens litter decomposing at four European field sites. *Plant Ecology* 154: 29–36.

Moore T & Basiliko N (2006) Decomposition in Boreal Peatlands. In: Wieder R K & Vitt D H (eds) *Boreal Peatland*

Ecosystems. Ecological Studies, Vol. 188. Springer-Verlag Berlin Heidelberg, Germany.

Morgan P B, Ainsworth E A & Long S P (2003) How does elevated ozone impact soybean? A meta-analysis of photosynthesis, growth and yield. *Plant, Cell and Environment* 26: 1317–1328.

Morré D J, Selldén G, Ojanperä K, Sandelius A S, Egger A, Morré D M, Chalko C M & Chalko R A (1990) Peroxisome proliferation in Norway spruce induced by ozone. *Protoplasma* 155: 58–65.

Mörsky S K, Haapala J K, Rinnan R, Tiiva P, Saarnio S, Silvola J, Holopainen T & Martikainen P J (2008) Long-term ozone effects on vegetation, microbial community and methane dynamics of boreal peatland microcosms in open-field conditions. Global *Change Biology* 14: 1891–1903.

Mörsky S K, Haapala J K, Rinnan R, Saarnio S, Kyrö E, Silvola J, Martikainen P J & Holopainen T. Transient effects of elevated UV-B radiation on UV-absorbing pigments but no effects on leaf anatomy of a sedge *Eriophorum russeolum* in a long-term field exposure study. Manuscript.

Newsham K K & Robinson S A (2009) Responses of plants in polar regions to UVB exposure: a meta-analysis. *Global Change Biology* 15: 2574–2589.

Niemi R, Martikainen P J, Silvola J, Wulff A, Turtola S & Holopainen T (2002a) Elevated UV-B radiation alters fluxes of methane and carbon dioxide in peatland microcosms. *Global Change Biology* 8: 361–371.

Niemi R, Martikainen P J, Silvola J & Holopainen T (2002b) Ozone effects on Sphagnum mosses, carbon dioxide exchange and methane emission in boreal peatland microcosms. *The Science of Total Environment* 289: 1–12.

Nikolova P S, Andersen C P, Blaschke H, Matyssek R & Häberle KH (2010) Belowground effects of enhanced tropospheric ozone and drought in a beech/spruce forest (*Fagus sylvatica* L./*Picea abies* [L.] Karst). *Environmental Pollution* 158: 1071–1078.

Nikula S, Percy K, Oksanen E, Holopainen T & Manninen S (2009) Effects of elevated ozone on growth and foliar traits of European and hybrid aspen. *Boreal Environmental Research* 14 suppl. A: 29–47.

Novak K, Schaub M, Fuhrer J, Skelly J M, Hug C, Landolt W, Bleuler P & Kräuchi N K (2005) Seasonal trends in reduced leaf gas exchange and ozone-induced foliar injury in three ozone sensitive woody plant species. *Environmental Pollution* 136: 33–45.

Nussbaum S, Geissmann M, Eggenberg P, Strasser R J & Fuhrer J (2001) Ozone sensitivity in herbaceous species as assessed by direct and modulated chlorophyll fluorescence techniques. *Journal of Plant Physiology* 158: 757–766.

Oksanen E, Sober J & Karnosky D F (2001) Impacts of elevated CO_2 and/or O_3 on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environmental Pollution* 115: 437–446.

Oksanen E, Häikiö E, Sober J & Karnosky D F (2003) Ozone-induced H_2O_2 accumulation in field-grown aspen and birch is linked to foliar ultrastructure and peroxisomal activity. *New Phytologist* 161: 791–799.

Overmyer K, Brosché M & Kangasjärvi J (2003). Reactive oxygen species and hormonal control of cell death. *Trends in Plant Science* 8: 335–342.

Pancotto V A, Sala O E, Cabello M, López 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 Biology* 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 Biology* 11: 1982–1989.

Paoletti E & Grulke N E (2005) Does living in elevated CO_2 ameliorate tree response to ozone? A review on stomatal responses. *Environmental Pollution* 137: 483–493.

Paoletti E & Grulke N E (2010) Ozone exposure and stomatal sluggishness in different plant physiognomic classes. *Environmental Pollution* 158: 2664–2671.

Pell E J, Schlagnhaufer C D 6 Arteca R N (1997) Ozone-induced oxidative stress: mechanisms of action and reaction. *Physiologia Plantarum* 100: 264–273.

Phillips R L, Zak D R, Holmes W E & White D C (2002) Microbial community composition and function beneath temperate trees exposed to elevated atmospheric carbon dioxide and ozone. *Oecologia* 131: 236–244.

Pleijel H & Danielson H (1997) Growth of 27 herbs and grasses in relation to ozone exposure and plant strategy. *New Phytologist* 135: 361–367.

Pleijel H, Danielsson H, Ojanperä K, De Temmerman L, Högy P, Badiani M & Karlsson P E (2004) Relationships between ozone exposure and yield loss in European wheat and potato—a comparison of concentration- and flux-based exposure indices. *Atmospheric Environment* 38: 2259–2269.

Potter L, Foot J P, Caporn J & Lee J A (1996) The effects of long-term elevated ozone concentrations on the growth and photosynthesis of *Sphagnum recurvum* and *Polytrichum commune*. *New Phytologist* 134: 649–656.

Power S A & Ashmore M R (2002) Responses of fen and fen-meadow communities to ozone. *New Phytologist* 156: 399–408.

Pääkkönen E, Holopainen T & Kärenlampi L (1995) Aging-related anatomical and ultrastructural changes in leaves of birch (*Betula pendula* Roth.) clones as affected by low ozone exposure. *Annals of Botany* 75: 285–294.

Ranieri A, Guintini D, Ferraro F, Nali C, Baldan B, Lorenzini G & Soldatini G F (2001) Chronic ozone fumigation induces alterations in thylakoid functionality and composition in two poplar clones. *Plant Physiology and Biochemistry* 39: 999–1008.

Reiling K & Davison A W (1994) Effects of exposure to ozone at different stages in the development of *Plantago major* L. on

chlorophyll fluorescence and gas exchange. *New Phytologist* 128: 509–514.

Riikonen J, Holopainen T, Oksanen E & Vapaavuori E (2005) Leaf photosynthetic characteristics of silver birch during three years of exposure to elevated concentrations of CO_2 and O_3 in the field. *Tree Physiology* 25: 621–632.

Rinnan R, Impiö M, Silvola J, Holopainen T & Martikainen P J (2003) Carbon dioxide and methane fluxes in boreal peatland microcosms with different vegetation cover - effects of ozone or ultraviolet-B exposure. *Oecologia* 137: 475–483.

Rinnan R & Holopainen T (2004) Ozone Effects on the ultrastructure of peatland plants: Sphagnum mosses, *Vaccinium oxycoccus*, *Andromeda polifolia* and *Eriophorum vaginatum*. *Annals of Botany* 94: 623–634.

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 Biology* 11: 564–574.

Rinnan R, Gehrke C & Michelsen A (2006) Two mire species respond differently to enhanced ultraviolet-B radiation: effects on biomass allocation and root exudation. *New Phytologist* 169: 809–818.

Rinnan R, Nerg A-M, Ahtoniemi P, Suokanerva H, Holopainen T, Kyrö E & Bååth E (2008) Plant-mediated effects of elevated ultraviolet-B radiation on peat microbial communities of a subarctic mire. *Global Change Biology* 14: 925–937.

Riutta T, Laine J, Aurela M, Rinne J, Vesala T, Laurila T, Haapanala S, Pihlatie M 6 Tuittila E-S (2007) Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. *Tellus* 59B: 838–852.

Royal Society (2008) *Ground-level ozone in the 21st century: future trends, impacts and policy implications*, Science Policy, 15/08. The Royal Society, London, UK.

Rozema J, Tosserams M, Nelissen H J M, van Heerwaarden L, Broekman R A & Flierman N (1997) Stratospheric ozone reduction and ecosystem processes: enhanced UV-B radiation affects chemical quality and decomposition of leaves of the dune grassland species *Calamagrostis epigeios*. *Plant Ecology* 128: 285–294.

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. *Environmental Pollution* 137: 428–442.

Ruimy A P, Jarvis D, Baldocchi D 6 Saugier B (1996) CO_2 fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research* 26: 1–68.

Rämö K, Kanerva T, Nikula S, Ojanperä K & Manninen S (2006) Influences of elevate ozone and carbon dioxide in growth responses of lowland hay meadow mesocosms. *Environmental Pollution* 144: 101–111.

Saarinen T (1996) Biomass and production of two vascular plants in a boreal mesotrophic fen. *Canadian Journal of Botany* 74: 934–938.

Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H & Martikainen P J (1997). Seasonal variation in CH_4 emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. *Oecologia* 110: 414–422.

Saarnio S, Järviö S, Saarinen T, Vasander H & Silvola J (2003) Minor changes in vegetation and carbon gas balance in a boreal mire under a raised CO_2 or NH_4NO_3 supply. *Ecosystems* 6: 46–60.

Saarnio S, Wittenmayer L & Merbach W (2004) Rhizospheric exudation of *Eriophorum vaginatum* L. - potential link to methanogenesis. *Plant and Soil* 267: 343–355.

Saarnio S, Morero M, Shurpali N J, Tuittila E-S, Mäkilä M & Alm J (2007) Annual CO_2 and CH_4 fluxes of pristine boreal mires as a background for the lifecycle analyses of peat energy. *Boreal Environment Research* 12: 101–113.

Santos I, Fidalgo F, Almeida J M & Salema R (2004) Biochemical and ultrastructural changes in leaves of potato plants grown under supplementary UV-B radiation. *Plant Science* 167: 925–935.

Scagel C F & Andersen C P (1997) Seasonal changes in root and soil respiration of ozone-exposed ponderosa pine (*Pinus ponderosa*) grown in different substrates. *New Phytologist* 136: 627–643.

Schraudner M, Langebartels C & Sandermann H (1997) Changes in the biochemical status of plant cells induced by the environmental pollutant ozone. *Physiologia Plantarum* 100: 274-280.

Searles P S, Flint S D & Caldwell M M (2001a) A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127: 1–10.

Searles P S, Kropp B R, Flint S D & Caldwell M M (2001b) Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. *New Phytologist* 152: 213–221.

Searles P S, Flint S D, Díaz S B, Rousseaux M C, Ballaré C L & Caldwell M M (2002) Plant response to solar ultraviolet-B radiation in a southern South American *Sphagnum* peatland. *Journal of Ecology* 90: 704–713.

Shannon R D, White J R, Lawson J E & Gilmour B S (1996) Methane efflux from emergent vegetation in peatlands. *Journal of Ecology* 84: 239–246.

Sitch S, Cox P M, Collins W J & Huntingford C (2007) Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature* 448: 791–794.

Smith W K, Gao W, Steltzer H, Wallenstein M D & Tree R (2010) Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Global Change Biology* 16: 484–495.

Sutinen S, Skärby L, Wallin G & Selldén G (1990) Long-term exposure of Norway spruce, *Picea abies* (L.) Karst., to ozone in open-top chambers II. Effects on the ultrastructure of needles. *New Phytologist* 115: 345–355.

Tevini M & Steinmüller D (1985) Composition and function of plastoglobuli. 2. Lipid-composition of leaves and plastoglobuli during beech leaf senescence. *Planta* 163: 91–96.

Thomas K L, Benstead J, Davies K L & Lloyd D (1996) Role of wetland plants in the diurnal control of CH_4 and CO_2 fluxes in peat. *Soil Biology and Bioshemistry* 28: 17–23.

Tiiva P, Rinnan R, Faubert P, Räsänen J, Holopainen T, Kyrö E & Holopainen J K (2007) Isoprene emission from a subarctic peatland under enhanced UV-B radiation. *New Phytologist* 176:346–55.

Timonen U, Huttunen S & Manninen S (2004) Ozone sensitivity of wild field layer plant species of northern Europe. A review. *Plant Ecology* 172: 27–39.

Toet S, Ineson P, Peacock S & Ashmore M (2011) Elevated ozone reduces methane emissions from peatland mesocosms. *Global Change Biology* 17: 288–296.

Turunen J, Tomppo E, Tolonen K & Reinikainen A (2002) Estimating carbon accumulation rates of undrained mires in Finland - application to boreal and subarctic regions. *The Hologene* 12: 69–80.

Utriainen J, Janhunen S, Helmisaari H-S & Holopainen T (2000) Biomass allocation, needle structural characteristics and nutrient composition in Scots pine seedlings exposed to elevated CO_2 and O_3 concentrations. *Trees* 14: 475–484.

Valkama E, Kivimäenpää M, Hartikainen H & Wulff A (2003) The combined effects of enhanced UV-B radiation and selenium on growth, chlorophyll fluorescence and ultrastructure in strawberry (*Fragaria × ananassa*) and barley (*Hordeum vulgare*) treated in the field. *Agricultural and Forest Meteorology* 120: 267–278.

Vasander H & Kettunen A (2006) Carbon in Boreal Peatlands. In: Wieder R K & Vitt D H (eds) *Boreal Peatland Ecosystems*. Ecological Studies, Vol. 188. Springer-Verlag Berlin Heidelberg, Germany. Pages 165–194.

Vingarzan R (2004) A review of surface ozone background levels and trends. *Atmospheric Environment* 38: 3431–3442.

Vitt D H (2006) Functional characteristics and indicators of boreal peatlands. In: Wieder R K & Vitt D H (eds) *Boreal Peatland Ecosystems*. Ecological Studies, Vol. 188. Springer-Verlag Berlin Heidelberg, Germany. Pages 9–24.

Volk M, Obrist D, Novak K, Giger R, Bassin S & Fuhrer J (2011) Subalpine grassland carbon dioxide fluxes indicate substantial carbon losses under increased nitrogen deposition, but not at elevated ozone concentration. *Global Change Biology* 17: 366–376.

Wallén B (1986) Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. *Oikos* 46: 51–56.

Williamson J, Mills G & Freeman C (2010) Species-specific effects of elevated ozone on wetland plants and decomposition processes. *Environmental Pollution* 158: 1197–1206.

Wittig V E, Ainsworth E A & Long S (2007) To what extend do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant, Cell and Environment* 30: 1150–1162.

WMO (World Meteorological Organization) (2007) *Scientific assessment of ozone depletion: 2006*. Global Ozone Research and Monitoring Project—Report No. 50. Geneva, Switzerland.

Wulff A, Ahonen J & Kärenlampi L (1996) Cell ultrastructural evidence of accelerated ageing of Norway spruce needles in industrial areas. *New Phytologist* 133: 553–561.

Wulff A, Anttonen S, Pellinen R, Savonen E-M, Sutinen M-L, Heller W, Sandermann H Jr. & Kangasjärvi J (1999) Birch (*Betula pendula* Roth.) responses to high UV-B radiation. *Boreal Environment Research* 4: 77–88.

Xiong F S & Day T A (2001) Effect of solar ultraviolet-B radiation during springtime ozone depletion on photosynthesis and biomass production of antarctic vascular plants. *Plant Physiology* 125: 738–751.

Yamaji K, Julkunen-Tiitto R, Rousi M, Freiwald V & Oksanen E (2003) Ozone exposure over two growing seasons alters root-to-shoot ratio and chemical composition of birch (*Betula pendula* Roth). *Global Change Biology* 9: 1363–1377.

Yoshida L C, Gamon J A & Andersen C P (2001) Differences in above- and below-ground responses to ozone between two populations of a perennial grass. *Plant and Soil* 223: 203–211.

Yu S-G & Björn L O (1999) Ultraviolet-B stimulates grana formation in chloroplasts in the African desert plant *Dimorphotheca pluvialis*. *Journal of Photochemistry and Photobiology B: Biology* 49: 65–70.

Zaller J G, Caldwell M M, Flint S D, Scopel A L, Sala O E, Ballaré C L (2002) Solar UV-B radiation affects below-ground parameters in a fen ecosystem in Tierra del Fuego, Argentina: implications of stratospheric ozone depletion. *Global Change Biology* 8: 867–871.

Zu Y-G, Pang H-H, Yu J-H, Li D-W, Wei X-X, Gao Y-X & Tong L (2010) Responses in the morphology, physiology and biochemistry of *Taxus chinensis* var. *mairei* grown under supplementary UV-B radiation. *Journal of Photochemistry and Photobiology B: Biology* 98: 152–158.

Jaana Haapala
Mire plants and carbon dioxide dynamics under increased tropospheric ozone concentration and UV-B radiation

The aim of this thesis was to investigate the long-term effects of increasing tropospheric ozone concentration and supplemental UV-B radiation on carbon dioxide dynamics of boreal mire ecosystems. Effects of these stressors were studied separately in two multi-year experiments under open-field conditions. The presented results demonstrate the importance of long-term experiments in natural conditions in the effort to assess the magnitude of ecosystem level responses to these two stress factors.

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