TEXTE
71/2015

Assessment of the impacts of ozone on biodiversity in terrestrial ecosystems: Literature review and analysis of methods and uncertainties in current risk assessment approaches

Part II: Literature review of the current state of knowledge on the impact of ozone on biodiversity in terrestrial ecosystems

For our Environment

Umwelt
Bundesamt

TEXTE 71/2015

Environmental Research of the
Federal Ministry for the
Environment, Nature Conservation,
Building and Nuclear Safety

Project No. (FKZ) 3711 63 235
Report No. (UBA-FB) 002142/2,E

Assessment of the impacts of ozone on biodiversity in terrestrial ecosystems: Literature review and analysis of methods and uncertainties in current risk assessment approaches

Part II: Literature review of the current state of knowledge on the impact of ozone on biodiversity in terrestrial ecosystems

by

Elke Bergmann, Jürgen Bender, Hans-Joachim Weigel
Thünen-Institut für Biodiversität, Braunschweig

On behalf of the Federal Environment Agency (Germany)

Imprint

Publisher:
Umweltbundesamt
Wörlitzer Platz 1
06844 Dessau-Roßlau
Tel: +49 340-2103-0
Fax: +49 340-2103-2285
info@umweltbundesamt.de
Internet: www.umweltbundesamt.de

/umweltbundesamt.de
/umweltbundesamt

Study performed by:
Thünen Institute of Biodiversity
Bundesallee 50
38116 Braunschweig

Study completed in:
December 2014

Edited by:
Section II 4.3 Air pollution control and terrestrial ecosystems
Gudrun Schütze

Publication as pdf:
http://www.umweltbundesamt.de/en/publikationen/assessment-of-the-impacts-of-ozone-on-biodiversity

ISSN 1862-4804

Dessau-Roßlau, August 2015

The Project underlying this report was supported with funding from the Federal Ministry for the Environment, Nature Conservation, Building and Nuclear safety under project number FKZ 3711 63 235. The responsibility for the content of this publication lies with the author(s).

Contents

List of figures

List of tables

Index of abbreviations

A2, B1	simulated emission scenarios of the IPCC
AA	ambient air
BAI	basal area increment growth
CBD	Convention on Biological Biodiversity
CF	charcoal filtered air ≈ clean air
CONECOFOR	National Integrated Programme for Forest Ecosystem Monitoring (Italian acronym: CONtrolli ECOsistemi FORestali
CSR	competitive-stress tolerator- ruderal: ecological strategy modell of Grime (1979)
CSTR	continuously stirred-tank reactor
FACE	free air carbon dioxide enrichment
GPP	gross primary production
HR	hypersensitive reaction
ICP	International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects operating under the UNECE Convention on Long-range Transboundary Air Pollution
IPCC	Intergovernmental Panel on Climate Change
MRGR	mean relative growth rate
NF	non-filtered air ≈ ambient air
NPP	net primary production
OTC	open top chamber
ppb	part per billion
RGR	relative growth rate
ROS	reactive oxygen species
SLA	specific leaf area
UNECE	United Nations Economic Commission for Europe
VOC	volatile organic compounds

1 Introduction

1.1 Ozone pollution

During the last 60 years tropospheric or ground-level ozone has emerged as an air pollution problem of global dimension with respect to its harmful impacts on human health and vegetation (Royal Society 2008). As a secondary air pollutant ozone is formed in the troposphere through a number of sun-light driven photochemical reactions involving the main precursor substances nitrogen mono- and dioxide (NO/NO_2), volatile organic compounds (VOC), methane (CH_4) and carbon monoxide (CO) (Staehelin 2003). These precursors are produced naturally or emitted from anthropogenic activities such as vehicles, power plants, biomass burning and all other forms of combustion.

Naturally occurring ozone concentrations in the troposphere (ground-level) in the pre-industrial era have been described to range between approx. 5 – 20 parts per billion (ppb) (Marenco et al. 1994). Since the pre-industrial era the global annual mean background ozone concentrations have increased considerably to values between approx. > 20 - 45 ppb depending on the geographical location (Vingarzan 2004) with a rate of increase in the annual mean values ranging between 0.1 - 1.0 ppb per year. This increase has been observed over large areas of Europe and North America, and more recently in many countries in Asia (e.g. China, India, Pakistan), South America (e.g. Brazil) and Africa with rapidly emerging industrialization and hence, increasing emissions of precursors of ozone. In these countries, ozone has reached levels in ambient air which are of concern with respect to vegetation damage and human health effects (Emberson 2003; Royal Society 2008).

Future changes of the ozone levels will be determined by the trends of the emissions of the precursors and of temperature and solar radiation. While predictive models e.g. based on IPCC-SRES global emission scenarios indicate that background ozone concentrations will continue to increase at a rate of 0.5 % - 2 % per year in the Northern Hemisphere during the next 100 years and will be in the range of ca. 42 - 84 ppb by 2100 (Prather et al. 2003; Vingarzan 2004; Jacob & Winner 2009), within a recently published study more moderate increases of ozone levels until 2050 are predicted (Wild et al. 2012). By 2100, about 50 % of forests worldwide are expected to be exposed to ozone concentrations above 60 ppb (Percy et al. 2003a; Andersson & Engardt 2010).

Ozone concentrations influenced by human activities vary significantly with time (diurnally, seasonally, inter-annually) and with geographic location. This variability is of particular relevance for the effects on vegetation, as different vegetation types or developmental stages of plants, respectively, may be exposed to very different levels of ozone during the course of the year. As ozone formation is dependent on sunlight and as some of the chemical reactions involved in the ozone formation in the troposphere are temperature-dependent, ozone concentrations are particularly high at warm sunny days (Royal Society 2008). While at low elevation sites ozone concentrations show diurnal cycles with low concentrations during the night and in the morning and high and peak concentration during the afternoon, high elevation sites mostly do not show such distinct diurnal variation (Stockwell et al. 1997). In general, at a particular location the build-up of phytotoxic ozone concentrations depends on the local meteorology, the topography and the regional sources of ozone precursors. In Europe, the highest ozone levels occur in Central and Southern Europe (Royal Society 2008).

1.2 Effects of tropospheric ozone on biota

Ozone has significant impacts on human health, crop productivity, and ecosystems globally. Current ozone exposure levels in North America and Europe were related to respiratory health effects and lung function has been shown to be sensitive to both acute and long-term exposures (Royal Society 2008; EEA 2013; EPA 2013).

Terrestrial ecosystems are the major sink for tropospheric ozone and consequently, vegetation is at particular risk from this pollutant. Ozone enters the plant interior through the stomata and being a strong oxidant ozone and its breakdown products, respectively, are able to impact plants by altering plant cellular functions and by reducing photosynthesis and changing other important physiological functions. Collectively, this may result in visible leaf injury, growth and biomass reduction and overall inferior plant vigour (Ashmore 2005; Booker et al. 2009; Matyssek et al. 2010a; Matyssek et al. 2010b). In the past four decades ozone effects have been thoroughly investigated within crops (reviewed by e.g. Heagle 1989; Fiscus et al. 2005; Booker et al. 2009; Mills & Harmens 2011) and particularly within deciduous and coniferous trees (reviewed e.g. by Sandermann et al. 1997; Percy et al. 2003a; Matyssek et al. 2010a; Matyssek et al. 2010b; Matyssek et al. 2013). Other types of natural or semi-natural vegetation have only recently and to a lesser extent received attention (reviewed by e.g. Fuhrer 1997; Davison & Barnes 1998; Ashmore 2005).

Vegetation is an important natural sink for ozone. Ozone is transferred from the atmosphere onto plant canopies by turbulent diffusion (deposition), which is governed by micro-meteorological conditions (radiation, temperature, wind, etc.) and the roughness of the vegetation. The uptake of ozone by vegetation is attributed to both non-stomatal and stomatal deposition. Non-stomatal deposition includes deposition to soil, stems, cuticles and other external surfaces. It has long been known that penetration of ozone through the plants cuticle is of minor importance in comparison to the route of uptake through the stomata (Kerstiens & Lendzian 1989; Massman & Grantz 1995). This transfer of the gas through the atmosphere (turbulent diffusion) into the plant via molecular diffusion through the stomata is currently considered the key process in relating ozone exposure to plant responses (Fowler et al. 2009). Consequently, all environmental factors that modify the stomatal aperture (e.g. temperature, light and soil water conditions, other pollutants, atmospheric CO_2 concentration) and which thus affect leaf gas exchange have an influence on the uptake of ozone into the plant interior (Fiscus et al. 2005; Fuhrer 2009).

Field measurements of ozone deposition (flux) in various ecosystems indicate that total dry deposition is largely dominated by stomatal uptake during the most active parts of the growing season, but, at other times of the year and depending on vegetation type and weather conditions, non-stomatal deposition can be larger than stomatal uptake (Cieslik 2004; Cape et al. 2009).

Once ozone molecules have passed the stomatal pore its subsequent effects on the plant include reactions with the apoplastic fluid and generation of reactive oxygen species (ROS), effects on the cell membrane structure and function, changes of cell metabolism and cellular events, which finally result in the generation of observable plant responses like chlorotic or necrotic tissue damage, reduced photosynthesis, temporal shifts in the plant´s development, and losses in productivity (Cho et al. 2011; Dizengremel et al. 2013).

According to the present understanding the accumulation of ROS induces defence reactions that are similar other oxidative stress responses or pathogen attack and may result in a programmed cell death (hypersensitive response, HR), a process which is thought to have the biological significance of limiting the spreading of the oxidative burst (Langebartels et al. 2002; Wohlgemuth et al. 2002; Kangasjärvi et al. 2005; Bartoli et al. 2013). Defence mechanisms involved in detoxifying the ROS, directly or indirectly derived from ozone exposure, may consist in enzymatic and non-enzymatic reactions with the apoplastic ascorbate pool seems to be particular important (Fiscus et al. 2005; Iriti & Faoro 2008; Fuhrer 2009). Defence reactions require energy for regeneration of antioxidants, i.e. particularly at prolonged ozone exposure detoxification capacity may decline due to decreased rates of carbon assimilation and limited available energy (Wieser & Matyssek 2007). However, depending on the severity of oxidative stress and the detoxification capacity cell injury may occur either as HR-type or chlorotic symptoms.

Visible injury resulting from ambient ozone pollution has been observed on a wide range of plant species including trees, crops, and species of semi-natural vegetation in North-America and in Europe (see Flagler 1998; Innes et al. 2001; Mills et al. 2011). While on broad-leaved plants visible injuries include stippling, flecking, surface bleaching, bifacial necrosis, pigmentation (e.g., bronzing) and chlorosis, for conifers visible injury has been described as chlorotic banding, tip burn, flecking and chlorotic mottling. For both plant types ozone induced symptoms of premature senescence of leaves and needles, respectively, can be observed. These foliar lesions can vary between and within taxonomic groups and the degree and extent of visible foliar injury development may vary from year to year and site to site.

At chronic ozone exposure, visible injury is often not observed, but decreased rates of CO_2 assimilation indicate adverse effects of ozone on plant vitality. The response of photosynthesis to ozone has received much attention in order to explain ozone induced losses of plant productivity in a wide variety of tree and crop species as well as in grassland and other native plant species (Reich 1987; Morgan et al. 2003; Fiscus et al. 2005; Wittig et al. 2007; Booker et al. 2009). It may be assumed that plant growth retardation under longer-term ozone exposure at moderately enhanced concentrations is mostly the result of reduced rates of assimilation at the leaf level, although within-tree alterations of carbon allocation due to disturbed phytohormonal regulation have also been shown to affect tree growth (Winwood et al. 2007; Kitao et al. 2012). However, loss of carbon assimilation capacity is mostly considered as the primary reason for a decline of photosynthesis under ozone exposure. Although many different changes are observed in the photosynthetic apparatus, decreased activity and amount of the enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) appear to be the prevailing causes of loss of photosynthetic capacity.

There are no organisms within our terrestrial ecosystems other than vascular plants, which attract interest of ozone research that even begins to compare with them. A very few studies investigated respiratory and thermoregulatory behaviour of ozone-exposed vertebrates, namely amphibians and reptiles. Other vertebrate species acted as objects in relation to medical research studies. Likewise, experiments on microbes as part of post-harvest treatments of agricultural fruits with ozone appeared to be inappropriate in the ecological context applied to this study.

1.3 Methods to study ozone effects on plants

Experimental techniques to expose single plants, plant communities and segments of ecosystems to modified ozone concentrations range from controlled environmental chambers, greenhouses, field chambers up to open-air ozone exposure systems. Most of the information of the effects of ozone on plants is derived from the use of various types of indoor and outdoor chambers.

Laboratory fumigation chambers of various designs (e.g. continuously stirred-tank reactor chambers = CSTR, Heck et al. 1978) which provide highly reproducible environmental and ozone exposure conditions have widely been used for assessing visible injury or physiological and biochemical ozone effects. However, due to different microclimatic conditions in the chambers compared to open air ("chamber effects") plants often show morphological or physiological differences compared to field-grown plants.

Beginning in the 1980s, controlled environment exposure chambers had been replaced more and more by the technique of field-based open-top chambers (OTC, Heagle et al. 1973) which have been the most widely used ozone exposure system up to now (Heagle et al. 1988; Jäger et al. 1999; Oksanen et al. 2013; Zheng et al. 2013). This facility offered the opportunity to expose plants and model ecosystems for a whole season or even more and allowed to compare the effects of ambient (NF = non-filtered) or elevated levels of ozone to sub-ambient levels (CF = charcoal-filtered). Open-top chambers are best suited for in situ studies with low stature vegetation, e.g. like most crop or grassland species. To allow studies with taller trees large versions of OTCs have been constructed (Musselman & Hale 1997). According to Kolb & Matyssek (2001) chamber studies with trees cover only a short period of the entire life history of forest stands they are thus limited in predicting longer-term ecosystem effects of ozone.

Moreover, it has been observed that due to climatic differences OTCs may reduce the competitiveness of clover, and thereby alter the species composition (Fuhrer et al. 1994; Grünhage & Jäger 2003). In the late 1990s, the resulting necessity to avoid chamber effects, space limitations and restricted plant root volumes and to investigate established ecosystems in a more realistic ambient environment led to the utilisation of free-air exposure systems (Percy et al. 2010). The most often used chamberless exposure system for ozone effect studies is a modification of the circular free air carbon dioxide enrichment (FACE) system (Hendrey et al. 1999; Miglietta et al. 2001) which was modified to dispense ozone into plant canopies. During the last two decades large-scale FACE-type ozone exposure systems have been employed in ozone effects studies with crops like soybean, SoyFACE (Morgan et al. 2004) and young tree species, AspenFACE (Karnosky et al. 1999). A similar custom-designed circular free air ozone exposure system was used by Volk et al. (2003) in a Swiss grassland system. A free air ozone fumigation system in mature tree crowns of beech and spruce in Germany was developed by Werner & Fabian (2002) and tested and used by Matyssek et al. (2010a; (2010b; 2013). In free air ozone exposure systems the coupling between the atmosphere and the plant canopy as well as between the canopy and the respective soil volume largely remains unchanged. Thus, *in situ* water and nutrient fluxes at the ecosystem level can be investigated. Ideally, FACE-type ozone exposure systems allow ozone effect research at various hierarchical levels, i.e. to link molecular biology with eco-physiological research. Admittedly, within FACE-type exposure facilities, the fumigation regime necessarily based on the current ambient conditions and ozone exposure only consists in controlled enhancement of ozone levels in ambient air and the reference treatment could not be controlled. Therefore, the absence of an ozone effect could also reflect the exceedance of the thresholds in the control treatment and, consequently, the response would be underestimated. At least, when using established ecosystems any interpretation of changes entails all difficulties arising from the heterogeneity in soil conditions or plant growth combined with environmental factors both at a spatial and temporal scale (Stampfli & Fuhrer 2010). Another chamberless method to assess effects of ambient ozone levels on plants is represented by the use of protecting chemicals against ozone stress (Manning et al. 2011), which recently has been utilised on crops in Europe (Mills & Harmens 2011), and Asia (Rai & Agrawal 2012; Oksanen et al. 2013) or on trees (Paoletti et al. 2007b; Paoletti et al. 2011).

Among the methods of ozone exposure where there is no manipulation of the ozone concentration surrounding the plants are **ambient gradient studies**. Plants or plant community responses are examined along gradients of ozone concentrations across a landscape or regional transect providing multiple levels of exposure to ozone that are naturally occurring. Forest tree species and ecosystem responses to ozone have been assessed using gradient studies in the USA (Miller & McBride 1999; McLaughlin et al. 2007a), the Carpathian Mountains (Bytnerowicz et al. 2003), and in Italy (Ferretti et al. 2005b). Thus, for any experimental exposure the experimental design should be considered when interpreting results achieved.

1.4 Biological diversity and ecosystem services

Diversity is characteristic of all biological systems (Barker & Tingey 1992a) and conservation of biological diversity has become a major purpose in environmental policy. Prime threats to biodiversity conservation have acknowledged existing in land-use change, climate change, and invasive species. More recently, transboundary air pollution has been identified as a widespread problem, which should be included in the consideration of conservational issues.

The Convention on Biological Biodiversity (CBD) defined:

three main objectives

- The conservation of biological diversity
- The sustainable use of the components of biological diversity
- The fair and equitable sharing of the benefits arising out of the utilization of genetic resources

the use of the term "biological diversity"

> "…the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems"

http://www.cbd.int/convention/text/default.shtml

There are three levels of biological diversity which should be considered separately: ecosystem diversity, species diversity and genetic diversity. With respect to its vulnerability by air pollutants species and genetic diversity seem to be the most important one.

Species diversity

"The components of species diversity include the number of species present (species richness), their relative abundances (species evenness), the particular species present (species composition), the interactions among species (non-additive effects), and the temporal and spatial variation in these properties" (Chapin et al. 2000).

Ecosystem characteristics are not simply be determined by the presence or absence of species but rather by interactions among species as most ecosystem processes are non-additive functions of the traits of two or more species (Chapin et al. 2000). Species diversity determines the organismal traits and thereby determines functional properties of an ecosystem. In this context, function refers to processes within the ecosystem. Air pollution alters the function of the ecosystems when elemental cycles of the energy flow are altered. This alteration can also be manifested in changes in the biotic compositions of ecosystems. Diversity is believed to provide biological systems with the ability to adapt and respond to environmental changes (Barker & Tingey 1992b). As a consequence, any change in biodiversity will have profound consequences for ecosystem functioning and ecosystem resilience to environmental changes, which in turn may have economic impacts through the provision of ecosystem goods and services to society. Ecosystem services are defined as the benefits the society obtain from ecosystems and describe processes that support human activity. Such services include the regulating quality of air, soil, and water and provision of goods such as food, timber and fresh water.

It is now widely acknowledged that biodiversity is affected by climate change, with negative consequences for food security. In recent years, several attempts have been made to quantify the impacts of changes in ecosystem services e.g. (Gornall et al. 2010; Hatfield et al. 2011; Newton et al. 2011; Tian et al. 2012). It is evidenced that evolutionary adaptations to warmer conditions already have occurred and genetic shifts have been observed to modulate local effects of climate change (Parmesan 2006). Thus, the CBD declared: "…according to the Millennium Ecosystem Assessment, climate change is likely to become one of the most significant drivers of biodiversity loss by the end of the century…" (http://www.cbd.int/climate/intro.shtml).

For **ozone** it is expected that effects on terrestrial biodiversity are likely where ever concentrations are above the threshold, thus the Royal Society (2008) proposed that the impact of ground level ozone on biological diversity should be considered as a new and emerging issue under the CBD. At its tenth meeting, the 'Conference of the Parties' adopted a decision "to invite relevant organizations to submit technical information on the impact of ground-level ozone on biodiversity" (New and emerging issues of Recommendation XIV/16[1]).

This poses the question on how biodiversity can be quantified and monitored especially with regard to spatial and temporal scales. Species richness, the total number of species in a community, is considered as an important measure of biodiversity in view of its ease in measurement for vascular plant species and its comparability across communities (Ferretti et al. 2006b). In Europe, this issue has been integrated into the vegetation assessment performed at Level II plots by the UNECE[2]. However, the relationship between species richness and ecosystem processes can't be expressed by a simple statistical function (Chapin et al. 2000).

Cape et al. (2008) pointed toward the time factor to be regarded when studying the response of a community instead of an individual species as changes in genetic composition may only appear after several generations. Already in the early 1990s, Musselman (1992) assumed that short-term exposure to air pollution at current ambient concentrations is unlikely to change noticeably parameters which describe diversity at a landscape level and that altering spatial arrangement might be detected only after decades of monitoring.

Moreover, investigation of ozone effects on intact communities and ecosystem processes needs experimental approaches to allow plants to grow under realistic climatic and edaphic conditions while ozone exposure may be controlled. Laurence & Andersen (2003) emphasised below ground processes to be critical to understand and concluded that "…in some cases, ecosystem function will be more important than biodiversity, composition, or aesthetics".

1.5 Content of this report

The above mentioned difficulties in the experimental setup, long-term scale and the complexity in interacting species and functions, may explain the lack of studies which referred directly to the issue of biodiversity changes due to ozone. However, over the last decades the response of hundreds of plant species to ozone has been investigated in Europe, America and Asia and there exist a remarkable knowledge about biochemical and physiological mechanisms of ozone impact on vegetation.

Because interspecific variation in resistance to a pollutant such as ozone may act as a selecting factor, the first aim of this study was to give a comprehensive overview on species whose susceptibility to ozone at ambient or elevated concentrations has been tested under near-ambient conditions (chapter 3). A systematical identification and listing of sensitive/tolerant genotypes enables a first evaluation of a risk to biodiversity. For example, in terms of agro-biodiversity, prolonged impact of ozone may cause a restriction in the genetic

---

[1] http://www.cbd.int/recommendation/sbstta/default.shtml?id=12263

[2] http://www.unece.org/env/lrtap/workinggroups/wge/forests.html

diversity of cultivars of crops cultivated in the future (Weigel et al. 2011). Additionally to crops, native herbaceous and woody plant species we were also interested in reports describing ozone responses of non-plant species.

Substantial changes in traits of an ecosystem such as trophic relationships are expected, if ozone triggers the succession towards a more tolerant community. Therefore, in chapter 4 we will report on evidence about whether selection has already occurred either at clonal (individual) or provenance (population) levels.

Within the last few decades the focus was laid on the response of an ecosystem as a whole and the way by which ozone may interfere with interactions among species. Species interactions, including inter- and intraspecific plant competition, plant-microbes and plant-animal interactions may affect ecosystem processes directly by modifying processes e.g. pathways of energy and material flow or indirectly by modifying the abundances of species. Therefore, in chapter 5, we will report on the knowledge of how ozone may interfere with biotic interactions with focus on plant competition, herbivory insects, and plant pathogens. Further on, we will review on below-ground effects with a focus on the diversity of soil-born microbes and invertebrates, which are known to influence ecosystem productivity and cycling and storage of carbon, nutrients significantly.

The studies taken as a basis for all these items are not designated to quantify the degree of impacts in relation to the ozone concentration level but rather will give an overview over the broad spectrum of impacts on species and interactions. To assess ecosystem functions and services ozone-induced effects could be translated from the plant level to the ecosystem level and thus it will further be reported on the physiological basis and attempts to model effects of ozone on soil carbon and water in a quantitative way. Here, effects which are associated with the type of land use (e.g. pollination) will be discussed in chapter 6.

A final chapter applies to holistic approaches to study ecosystem effects in the field i.e. field survey studies that refer to ecological effects under ambient exposure levels that vary on a spatial scale. Long-term studies and network programs from America (e.g. The Bernardino Mountains Network Study) and Europe (the Carpathian Mountains Study and CONECOFORE in Italy) are analysed and results of several forest condition surveys will be presented (chapter 7.3).

1.6 References

Andersson, C. & Engardt, M. (2010): European ozone in a future climate: Importance of changes in dry deposition and isoprene emissions. Journal of Geophysical Research-Atmospheres 115, DOI: 10.1029/2008jd011690

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

Barker, J. T. & Tingey, D. T., editors (1992a): Air Pollution Effects on Biodiversity. Van Nostrand Reinhold, New York.

Barker, J. T. & Tingey, D. T. (1992b): The Effects of Air Pollution on Biodiversity: A Synopsis. In: Air Pollution Effects on Biodiversity (ed. by J. R. Barker &D. T. Tingey), Van Nostrand Reinhold, New York, pp. 3-9.

Bartoli, G., Forino, L. M. C., Tagliasacchi, A. M. & Durante, M. (2013): Cell death induced by ozone stress in the leaves of Populus deltoides x maximowiczii. Biologia Plantarum 57, 514-524.

Booker, F., Muntifering, R., McGrath, M., Burkey, K., Decoteau, D., Fiscus, E., Manning, W., Krupa, S., Chappelka, A. & Grantz, D. (2009): The ozone component of global change: Potential effects on agricultural and horticultural plant yield, product quality and interactions with invasive species. Journal of Integrative Plant Biology 51, 337-351.

Bytnerowicz, A., Badea, O., Barbu, I., Fleischer, P., Fraczek, W., Gancz, V., Godzik, B., Grodzinska, K., Grodzki, W., Karnosky, D., Koren, M., Krywult, M., Krzan, Z., Longauer, R., Mankovska, B., Manning, W. J., McManus, M., Musselman, R. C., Novotny, J., Popescu, F., Postelnicu, D., Prus-Glowacki, W., Skawinski, P., Skiba, S., Szaro, R., Tamas, S. & Vasile, C.

(2003): New international long-term ecological research on air pollution effects on the Carpathian Mountain forests, Central Europe. Environment International 29, 367-376.

Cape, J. N., Hamilton, R. & Heal, M. R. (2009): Reactive uptake of ozone at simulated leaf surfaces: Implications for 'non-stomatal' ozone flux. Atmospheric Environment 43, 1116-1123.

Cape, J. N., Bassin, S., Fuhrer, J., Gerosa, G., Alonso, R., Gimeno, B., Grünhage, L., Mikkelsen, T. N. & Mills, G. (2008): Challenges in understanding the risks to natural and semi-natural vegetation from ozone exposure. Italian Journal of Agronomy 3, 53-59.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. & Diaz, S. (2000): Consequences of changing biodiversity. Nature 405, 234-242.

Cho, K., Tiwari, S., Agrawal, S. B., Torres, N. L., Agrawal, M., Sarkar, A., Shibato, J., Agrawal, G. K., Kubo, A. & Rakwal, R. (2011): Tropospheric Ozone and Plants: Absorption, Responses, and Consequences. In: Reviews of Environmental Contamination and Toxicology (ed. by D. M. Whitacre), Vol 212 pp. 61-111.

Cieslik, S. A. (2004): Ozone uptake by various surface types: a comparison between dose and exposure. Atmospheric Environment 38, 2409-2420.

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

Dizengremel, P., Jolivet, I., Tuzet, A., Ranieri, A. & LeThiec, D. (2013): Integrative leaf-level phytotoxic ozone dose assessment and forest risk modelling. In: Climate Change, Air Pollution and Global Challenges, Vol 13. Developments in Environmental Science (ed. by R. Matyssek, N. Clarke et al.), Elsevier, pp. 267–282.

EEA, European Environment Agency (2013): Air quality in Europe — 2013 report (ed. by E. Report), Luxembourg: Publications Office of the European Union.

Emberson, L. (2003): Air pollution impacts on crops and forests: an introduction. Imperial College Press, London, UK.

EPA, United States Environmental Protection Agency (2013): Integrated Science Assessment for Ozone and Related Photochemical Oxidants. National Center for Environmental Assessment-RTP Division Research Triangle Park, NC

Ferretti, M., Bussotti, F., Fabbio, G. & Petriccione, B. (2005): Status and change of key ecosystem attributes monitored at the CONECOFOR plots, 1995-2005 - Achievements, problems, perspectives. Annali dell'Istituto Sperimentale per la Selvicoltura 34, 115-120.

Ferretti, M., Bussotti, F., Campetella, G., Canullo, R., Chiarucci, A., Fabbio, G. & Petriccione, B. (2006): Biodiversity - its assessment and importance in the Italian programme for the intensive monitoring of forest ecosystems CONECOFOR. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 3-16.

Fiscus, E. L., Booker, F. L. & Burkey, K. O. (2005): Crop responses to ozone: uptake, modes of action, carbon assimilation and partitioning. Plant Cell and Environment 28, 997-1011.

Flagler, R. B.,editors (1998): Recognition of air pollution injury to vegetation: a pictorial atlas. Air & Waste Management Association, 160 p.

Fowler, D., Pilegaard, K., Sutton, M. A., Ambus, P., Raivonen, M., Duyzer, J., Simpson, D., Fagerli, H., Fuzzi, S., Schjoerring, J. K., Granier, C., Neftel, A., Isaksen, I. S. A., Laj, P., Maione, M., Monks, P. S., Burkhardt, J., Daemmgen, U., Neirynck, J., Personne, E., Wichink-Kruit, R., Butterbach-Bahl, K., Flechard, C., Tuovinen, J. P., Coyle, M., Gerosa, G., Loubet, B., Altimir, N., Gruenhage, L., Ammann, C., Cieslik, S., Paoletti, E., Mikkelsen, T. N., Ro-Poulsen, H., Cellier, P., Cape, J. N., Horvath, L., Loreto, F., Niinemets, U., Palmer, P. I., Rinne, J., Misztal, P., Nemitz, E., Nilsson, D., Pryor, S., Gallagher, M. W., Vesala, T., Skiba, U., Brueggemann, N., Zechmeister-Boltenstern, S., Williams, J., O'Dowd, C., Facchini, M. C., de Leeuw, G., Flossman, A., Chaumerliac, N. & Erisman, J. W. (2009): Atmospheric composition change: Ecosystems-Atmosphere interactions. Atmospheric Environment 43, 5193-5267.

Fuhrer, J. (1997): Ozone sensitivity of managed pastures. In: Ecological Issues and Environmental Impact Assessment (ed. by P. N. Cheremisinoff), Gulf Publ Co, pp. 681-706.

Fuhrer, J. (2009): Ozone risk for crops and pastures in present and future climates. Naturwissenschaften 96, 173-194.

Fuhrer, J., Shariatmadari, H., Perler, R., Tschannen, W. & Grub, A. (1994): Effects of ozone on managed pasture .2. Yield, species composition, canopy structure, and forage quality. Environmental Pollution 86, 307-314.

Gornall, J., Betts, R., Burke, E., Clark, R., Camp, J., Willett, K. & Wiltshire, A. (2010): Implications of climate change for agricultural productivity in the early twenty-first century. Philosophical Transactions of the Royal Society B-Biological Sciences 365, 2973-2989.

Grünhage, L. & Jäger, H. J. (2003): From critical levels to critical loads for ozone: a discussion of a new experimental and modelling approach for establishing flux-response relationships for agricultural crops and native plant species. Environmental Pollution 125, 99-110.

Hatfield, J. L., Boote, K. J., Kimball, B. A., Ziska, L. H., Izaurralde, R. C., Ort, D., Thomson, A. M. & Wolfe, D. (2011): Climate impacts on agriculture: implications for crop production. Agronomy Journal 103, 351-370.

Heagle, A. S. (1989): Ozone and crop yield. Annual Review of Phytopathology 27, 397-423.

Heagle, A. S., Body, D. E. & Heck, W. W. (1973): An open-top field chamber to assess the impact of air pollution on plants. Journal of Environmental Quality 2, 365-368.

Heagle, A. S., Kress, L. W., Temple, P. J., Kohut, R. J., Miller, J. E. & Heggestad, H. E. (1988): Factors influencing ozone dose-yield response relationships in open-top chamber studies. Assessment of crop loss from air pollutants. Proceedings of an international conference, Raleigh, North Carolina, USA, 25-29 October 1987, pp. 141-179.

Heck, W. W., Philbeck, R. B. & Dunning, J. A. (1978): Continuous stirred tank reactor (CSTR) system for exposing plants to gaseous air contaminants - principles, specifications, construction, and operation. Agricultural Research Service Publication, Dept. of Agriculture, Southern Region.

Hendrey, G. R., Ellsworth, D. S., Lewin, K. F. & Nagy, J. (1999): A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO2. Global Change Biology 5, 293-309.

Innes, J., Skelly, J. & Schaub, H. (2001): Ozone and broadleaved species - A guide to the identification of ozne-induced foliar injury. Haupt, Birmensdorf, Eidgenössische Foschungsanstalt WSL. Bern, Stuttgart, Wien.

Iriti, M. & Faoro, F. (2008): Oxidative stress, the paradigm of ozone toxicity in plants and animals. Water Air and Soil Pollution 187, 285-301.

Jacob, D. J. & Winner, D. A. (2009): Effect of climate change on air quality. Atmospheric Environment 43, 51-63.

Jäger, H. J., Hertstein, U. & Fangmeier, A. (1999): The European Stress Physiology and Climate Experiment - project 1. Wheat (ESPACE-wheat): introduction, aims and methodology. European Journal of Agronomy 10, 155-162.

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

Karnosky, D. F., Mankovska, B., Percy, K., Dickson, R. E., Podila, G. K., Sober, J., Noormets, A., Hendrey, G., Coleman, M. D., Kubiske, M., Pregitzer, K. S. & Isebrands, J. G. (1999): Effects of tropospheric O-3 on trembling aspen and interaction with CO2: Results from an O-3-gradient and a face experiment. Water Air and Soil Pollution 116, 311-322.

Kerstiens, G. & Lendzian, K. J. (1989): Interactions between ozone and plant cuticles .1. Ozone deposition and permeability. New Phytologist 112, 13-19.

Kitao, M., Winkler, J. B., Low, M., Nunn, A. J., Kuptz, D., Haberle, K. H., Reiter, I. M. & Matyssek, R. (2012): How closely does stem growth of adult beech (Fagus sylvatica) relate to net carbon gain under experimentally enhanced ozone stress? Environmental Pollution 166, 108-115.

Kolb, T. E. & Matyssek, R. (2001): Limitations and perspectives about scaling ozone impacts in trees. Environmental Pollution 115, 373-392.

Langebartels, C., Wohlgemuth, H., Kschieschan, S., Grun, S. & Sandermann, H. (2002): Oxidative burst and cell death in ozone-exposed plants. Plant Physiology and Biochemistry 40, 567-575.

Laurence, J. A. & Andersen, C. P. (2003): Ozone and natural systems: understanding exposure, response, and risk. Environment International 29, 155-160.

Manning, W. J., Paoletti, E., Sandermann, H. & Ernst, D. (2011): Ethylenediurea (EDU): A research tool for assessment and verification of the effects of ground level ozone on plants under natural conditions. Environmental Pollution 159, 3283-3293.

Marenco, A., Gouget, H., Nedelec, P., Pages, J. P. & Karcher, F. (1994): Evidence of a long-term increase in tropospheric ozone from Pic du Midi data series - consequences - positive radiative forcing. Journal of Geophysical Research-Atmospheres 99, 16617-16632.

Massman, W. J. & Grantz, D. A. (1995): Estimating canopy conductance to ozone uptake from observations of evapotranspiration at the canopy scale and at the leaf scale. Global Change Biology 1, 183-198.

Matyssek, R., Clarke, N., Cudlin, P., Mikkelsen, T. N., Tuovinen, J. P., Wieser, G. & Paoletti, E.,editors (2013): Climate Change, Air Pollution and Global Challenges. Elsevier.

Matyssek, R., Karnosky, D. F., Wieser, G., Percy, K., Oksanen, E., Grams, T. E. E., Kubiske, M., Hanke, D. & Pretzsch, H. (2010a): Advances in understanding ozone impact on forest trees: Messages from novel phytotron and free-air fumigation studies. Environmental Pollution 158, 1990-2006.

Matyssek, R., Wieser, G., Ceulemans, R., Rennenberg, H., Pretzsch, H., Haberer, K., Loew, M., Nunn, A. J., Werner, H., Wipfler, P., Osswaldg, W., Nikolova, P., Hanke, D. E., Kraigher, H., Tausz, M., Bahnweg, G., Kitao, M., Dieler, J., Sandermann, H., Herbinger, K., Grebenc, T., Blumenroether, M., Deckmyn, G., Grams, T. E. E., Heerdt, C., Leuchner, M., Fabian, P. & Haeberle, K. H. (2010b): 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.

McLaughlin, S. B., Nosal, M., Wullschleger, S. D. & Sun, G. (2007): Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. New Phytologist 174, 109-124.

Miglietta, F., Peressotti, A., Vaccari, F. P., Zaldei, A., deAngelis, P. & Scarascia-Mugnozza, G. (2001): Free-air CO2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. New Phytologist 150, 465-476.

Miller, P. R. & McBride, J. R.,editors (1999): Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: A case study of the San Bernardino Mountains, Springer, New York NY.

Mills, G. & Harmens, H.,editors (2011): Ozone pollution: a hidden threat to food security. Report prepared by the ICP Vegetation. Centre for Ecology and Hydrology, Bangor.

Mills, G., Hayes, F., Simpson, D., Emberson, L., Norris, D., Harmens, H. & Bueker, P. (2011): Evidence of widespread effects of ozone on crops and (semi-)natural vegetation in Europe (1990-2006) in relation to AOT40-and flux-based risk maps. Global Change Biology 17, 592-613.

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.

Morgan, P. B., Bernacchi, C. J., Ort, D. R. & Long, S. P. (2004): An in vivo analysis of the effect of season-long open-air elevation of ozone to anticipated 2050 levels on photosynthesis in soybean. Plant Physiology 135, 2348-2357.

Musselman, R. & Hale, B. A. (1997): Methods for controlled and field ozone exposures of forest tree species in north america. In: Forest declione and ozone. A comparison of controlled chamber and field experiments (ed. by H. Sandermann, A. R. Wellburn &A. Heagle), Springer, pp. 277-315.

Musselman, R. C. (1992): Monitoring atmospheric effects on biological diversity. In: air pollution effects on biodiversity (ed. by J. R. Barker &D. T. Tingey), Van Nostrand Reinhold, New York, pp. 72-71.

Newton, A. C., Johnson, S. N. & Gregory, P. J. (2011): Implications of climate change for diseases, crop yields and food security. Euphytica 179, 3-18.

Oksanen, E., Pandey, V., Pandey, A. K., Keski-Saari, S., Kontunen-Soppela, S. & Sharma, C. (2013): Impacts of increasing ozone on Indian plants. Environmental Pollution 177, 189-200.

Paoletti, E., Contran, N., Manning, W. J. & Tagliaferro, F. (2007): Ethylenediurea (EDU) affects the growth of ozone-sensitive and tolerant ash (Fraxinus excelsior) trees under ambient O-3 conditions. Thescientificworldjournal 7, 128-133.

Paoletti, E., Manning, W. J., Ferrara, A. M. & Tagliaferro, F. (2011): Soil drench of ethylenediurea (EDU) protects sensitive trees from ozone injury. Iforest-Biogeosciences and Forestry 4, 66-68.

Parmesan, C. (2006): Ecological and evolutionary responses to recent climate change. In: Annual Review of Ecology Evolution and Systematics, Annual Reviews, Palo Alto, pp. 637-669.

Percy, K. E., Legge, A. H. & Krupa, S. V. (2003): Tropospheric ozone: A continuing threat to global forests? In: Air Pollution, Global Change and Forests in the New Millennium (ed. by D. F. Karnosky, K. E. Percy et al.), Elsevier, pp. 85-118.

Percy, K. E., Matyssek, R. & King, J. S. (2010): Facing the future: evidence from joint aspen FACE, soyFACE and SFB 607 Meeting. Environmental Pollution 158, 955-958.

Prather, M., Gauss, M., Berntsen, T., Isaksen, I., Sundet, J., Bey, I., Brasseur, G., Dentener, F., Derwent, R., Stevenson, D., Grenfell, L., Hauglustaine, D., Horowitz, L., Jacob, D., Mickley, L., Lawrence, M., von Kuhlmann, R., Muller, J. F., Pitari, G., Rogers, H., Johnson, M., Pyle, J., Law, K., van Weele, M. & Wild, O. (2003): Fresh air in the 21st century? Geophysical Research Letters 30, DPO: 10.1029/2002gl016285.

Rai, R. & Agrawal, M. (2012): Impact of Tropospheric Ozone on Crop Plants. Proceedings of the National Academy of Sciences India Section B-Biological Sciences 82, 241-257.

Reich, P. B. (1987): Quantifying plant response to ozone: a unifying theory. Tree Physiology 3, 63-91.

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

Sandermann, H., Wellburn, A. R. & Heath, R. L. (1997): Forest decline and ozone: synopsis. In: Forest Decline and Ozone: A Compariosn of Controlled Chamber and Field Experiments (ed. by H. Sandermann, A. R. Wellburn &R. L. Heath), Springer, pp. 369-377.

Staehelin, J. (2003): Ozone measurements and trends (troposphere). In: Encyclopedia of Physical Science and Technology (Third Edition, ed. by R. A. Meyers), Academic Press, New York, pp. 539-561.

Stampfli, A. & Fuhrer, J. (2010): Spatial heterogeneity confounded ozone-exposure experiment in semi-natural grassland. Oecologia 162, 515-522.

Stockwell, W. R., Kramm, G., Scheel, H. E., Mohnen, V. A. & Seiler, W. (1997): Ozone formation, destruction and exposure in Europe and the United States. In: Ecological Studies; Forest decline and ozone: A comparison of controlled chamber and field experiments (ed. by H. Sandermann, A. R. Wellburn &R. L. Heath), Springer-Verlag, Heidelberger Platz 3, D-1000 Berlin, Germany 175 Fifth Avenue, New York, New York 10010, USA, pp. 1-38.

Tian, H. Q., Chen, G. S., Zhang, C., Liu, M. L., Sun, G., Chappelka, A., Ren, W., Xu, X. F., Lu, C. Q., Pan, S. F., Chen, H., Hui, D. F., McNulty, S., Lockaby, G. & Vance, E. (2012): Century-Scale Responses of Ecosystem Carbon Storage and Flux to Multiple Environmental Changes in the Southern United States. Ecosystems 15, 674-694.

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

Volk, M., Geissmann, M., Blatter, A., Contat, F. & Fuhrer, J. (2003): Design and performance of a free-air exposure system to study long-term effects of ozone on grasslands. Atmospheric Environment 37, 1341-1350.

Weigel, H. J., Dauber, J. & Bender, J. (2011): Ground-level ozone - a threat for biodiversity? Gefahrstoffe Reinhaltung Der Luft 71, 98-102.

Werner, H. & Fabian, P. (2002): Free-air fumigation of mature trees - A novel system for controlled ozone enrichment in grown-up beech and spruce canopies. Environmental Science and Pollution Research 9, 117-121.

Wieser, G. & Matyssek, R. (2007): Linking ozone uptake and defense towards a mechanistic risk assessment for forest trees. New Phytologist 174, 7-9.

Wild, O., Fiore, A. M., Shindell, D. T., Doherty, R. M., Collins, W. J., Dentener, F. J., Schultz, M. G., Gong, S., MacKenzie, I. A., Zeng, G., Hess, P., Duncan, B. N., Bergmann, D. J., Szopa, S., Jonson, J. E., Keating, T. J. & Zuber, A. (2012): Modelling future changes in surface ozone: a parameterized approach. Atmospheric Chemistry and Physics 12, 2037-2054.

Winwood, J., Pate, A. E., Price, A. J. & Hanke, D. E. (2007): Effects of long-term, free-air ozone fumigation on the cytokinin content of mature beech trees. Plant Biology 9, 265-278.

Wittig, V. E., Ainsworth, E. A. & Long, S. P. (2007): To what extent 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.

Wohlgemuth, H., Mittelstrass, K., Kschieschan, S., Bender, J., Weigel, H. J., Overmyer, K., Kangasjarvi, J., Sandermann, H. & Langebartels, C. (2002): Activation of an oxidative burst is a general feature of sensitive plants exposed to the air pollutant ozone. Plant Cell and Environment 25, 717-726.

Zheng, F. X., Wang, X. K., Zhang, W. W., Hou, P. Q., Lu, F., Du, K. M. & Sun, Z. F. (2013): Effects of elevated O-3 exposure on nutrient elements and quality of winter wheat and rice grain in Yangtze River Delta, China. Environmental Pollution 179, 19-26.

2 Methods

2.1 Main literature database

A literature search has been performed and continuously expanded. Using the service of WEB OF SCIENCE™ relevant publications had been collected within the following databases: Web of Science ™ Core Collection, biological abstracts, and CAB Abstracts.

The following search criteria had been set in general for four different search profiles listed in Annex, Box 1:

time of publication:	1970 up to now
type of document	reviewed papers, research reports, or conference proceedings
excluded research fields:	post-harvest treatments, medical research, engineering, atmospheric chemistry and cognate disciplines.

The output results were selected individually for storing in a database (EndNote®) whether title of publication meet all requirements in fact. Exclusion criteria for example were papers which contain molecular issues on the mechanism of ozone toxicity or used non-relevant high ozone concentration levels (»200 ppb).

This pool of references was supplemented by relevant reports, cross-references and book chapters which are well-known within the research community and may have been publicised earlier than 1970, if helpful. From about 3000 references in total, about 1100 paper are included in his study, finally.

2.2 Criteria for publications used in chapter 3

A majority of publications had been collected in order to list sensitive taxa, however, for this chapter more specific recommendations were made:

- published not earlier than 1980
- studies on single plants or monocultures
- controlled exposure to ozone with at least two different levels of ozone
- exposure facilities: free-air fumigation systems, greenhouses, OTCs or, solardomes (hemispherical glasshouses)
- controlled environment studies are incorporated only, if hourly ozone concentration did not exceed 100 ppb, exceptions are indicated.

In chapters 3.1, 3.2, and 3.3 all worldwide available data about ozone responses of natural and semi-natural plant species, including pasture plant species will be presented. The following growth effects have been shown for native herbaceous species and are listed in table 1 to table 3 of Annex A, if available:

- general growth or yield reduction
- shoot, foliage, stem or root reduction
- reduction in no. or biomass of flowers
- flowering delay
- reduction in seed production
- reduction in germination rate of produced seeds
- decline of root/shoot ratio
- increase in shoot biomass
- increase in foliar biomass
- single leaf biomass increase

Symptoms of visible leaf injury have been described either as

- senescence,
- colouring,
- ozone specific symptoms,
- or have not been specified precisely
- yes or no (crops)

Data have been entered into an Excel® sheet. Effects were listed as either none, statistically significant or not significant, their significance was indicated. For native plants, further taxonomical information and distribution in Germany was according to BfN (Bundesamt für Naturschutz, http://www.floraweb.de/index.html).

3 Identifying ozone sensitive taxa

A central objective of this study is to give a comprehensive overview on the ozone susceptibility or tolerance, respectively, of any species belonging to terrestrial ecosystems which have been subjected to an assessment of its ozone sensitivity. These data have been compiled in order to allow both, to demonstrate the broadness of the spectrum of taxa included in ozone research and to exemplify the amplitude of inter- and intraspecific differences in ozone sensitive / tolerance. Thus, in this chapter a list will be provided presenting available data on woody plants, crops, and native herbaceous or pasture plants, for the main part. Although the overwhelming majority of studies was performed with vascular plant species, here, all non-plant species are also taken into account. Those taxa, whose response is causally related to the impact of ozone on a plant receptor e.g. invertebrates and microorganisms are covered by the topic of chapter 5 (biotic interactions).

To achieve this, a total of 418 references have been evaluated, which meet the requirements described in chapter 2. Effects were listed as either none, statistically significant or not significant indicated by brackets. It has to be noticed that by regarding all available references we were not always able to distinguish between studies but only between publications.

3.1 Native herbaceous and pasture plant species

In this chapter all worldwide available data about ozone responses of natural and semi-natural herbaceous plant species, including pasture plant species will be presented.

3.1.1 Overview on species investigated and their response to ozone

In total a number of 546 records giving information about 298 species belonging to 44 families have been found (Table 1 and Annex A, Table 1). There were 406 records referred to the occurrence of visible injuries and 356 records referred to growth parameters obtained from 62 publications, each having examined either one single species or up to 44 different species.

The majority of studies (documented by 38 publications) used OTCs or solardomes as exposure facility, whereas 13 publications reported on studies in controlled environment fumigation chambers. A summary of characteristics of species tested and the number of responsive species is given in Table 1. Out of all species which have been screened for their response to ozone, 198 were native to Germany (i.e. native, archaeophyte or neophyte) 14 species listed below are indicated as being endangered in Germany and 15 species are likely to be endangered[3]. About 60 % of species were perennials and 20 % of all species were grasses. Table 2 shows the proportion of responsive species applicable to different groups.

---

[3] Bundesamt für Naturschutz, Floraweb: http://www.floraweb.de/index.html

Table 1: Summary of assessments on native herbaceous or pasture plant species and their responses to ozone given as numbers of total records or species according to different descriptive groups.

	group	visible symptoms			growth effects			
		tested	total (sign.) spec./sen./col.	none	tested	reduction total (sign.)	increase total (sign.)	none
	total records	**406**	198 (30/34/5)	199	**356**	158(119)	21 (15)	177
	total species	**274**	147 (28/27/4)	154	**217**	114 (82)	19 (14)	126
functional type	herbs	**212**	111 (23/16/4)	115	**149**	85 (68)	13 (11)	79
	grasses	**56**	32 (3/10/0)	37	**59**	27 (20)	6 (3)	42
	sedges	**7**	4 (2/1/0)	2	**7**	2 (2)	0 (0)	5
life history	annuals or biennials	**101**	43 (4/8/0)	60	**48**	31 (23)	3 (2)	21
	perennials	**167**	102 (23/18/4)	92	**158**	75 (60)	16 (12)	103
relevance f. Germany	native to Germany[1]	**188**	107 (27/24/1)	107	**183**	93 (76)	18 (13)	113
	endangered[1]	**25**	10 (5/1/1)	17	**25**	7 (6)	3 (3)	18

(spec. = ozone specific, sen. = senescence, col.= coloured, sign., = significant). Sum of responsive and non-responsive species numbers is not equivalent to the total number of species assessed because of different results within different publications. All effects greater than 15 % were assumed to be significant, effects below 15 % as not significant.

[1] according to Bundesamt für Naturschutz, Floraweb: http://www.floraweb.de/index.html

Table 2: Proportion of responsive species (%) belonging to different descriptive groups. All symptoms and growth responses are combined. sign.= statistically significant.

group	injury		growth	
	sign.	total	sign.	total
total records	**49.0**	50.0	**37.4**	49.7
total species	**53.6**	54.4	**46.5**	59.0
herbs	**52.4**	53.3	**51.7**	63.8
grasses	**57.1**	57.1	**39.0**	52.5
annuals / biennials	**42.6**	43.6	**52.1**	68.8
perennials	**61.1**	61.7	**44.3**	55.1
native to Germany[1]	**56.4**	58.0	**47.0**	57.4
endangered species[1]	**40.0**	40.0	**36.0**	40.0

If studied repeatedly species may be assessed as both, responsive and not responsive, leading to sums >100 %. All effects greater than 15 % were assumed to be significant, effects below 15 % as not significant.

[1] according to Bundesamt für Naturschutz, Floraweb: http://www.floraweb.de/index.html

In total, for 177 species out of 293 a response to ozone has been documented. Across the whole data set, exactly half of all records evidenced significant impacts of ozone on herbaceous non-crop plants in terms of either visible leaf injury or growth responses. That means that about 53.5 % and 46.5 % of all species tested were found to express visible injury symptoms or changes in biomass production, respectively, in one experiment at least.

In terms of growth effects the proportion of sensitive species is higher for herbs than for grasses, however, the number of tested species belonging to herbs is 3.6 times higher than that of grasses.

A noticeable difference becomes obvious when considering the life history: regarding the parameter visible leaf injury the proportion of sensitive species is lower for annuals and biennials, but the proportion of species responding with impacts on growth is higher for annuals and biennials than for perennials.

There were seven families which were represented by at least ten different species in all ozone sensitivity studies Table 3. In terms of visible leaf injuries, six frequently studied families involved more than 50 % species classified to be sensitive for which the following order of decreasing sensitivity could be derived from the dataset: Onagraceae, Fabaceae, Cyperaceae, Lamiaceae, Asteraceae, and even though Poaceae. In terms of growth effects, again members of Fabaceae have been impaired by ozone by 70 % of the species and five more families are represented by about 40 % species being sensitive: Polygonaceae, Poaceae, Asteraceae, Lamiaceae, and Plantaginaceae. In conclusion, for both parameters, the exceptional status of legumes (Fabaceae) becomes obvious, as more than 70 % of species tested have been assessed to be sensitive, but a high proportion of members of Poaceae and Asteraceae are shown to respond sensitive to ozone. On the opposite, for crucifers (Brassicaceae) eight of nine species tested proved to be tolerant to ozone exposures.

Table 3: Frequency of sensitive and tolerant species in relation to their family classification: Total number of species tested and number of species showing a response to ozone (sign. = statistically significant).

family	total	visible injury	no visible symptoms	growth reduction total (sig.)	growth increase total (sig.)	no growth response
Apiaceae	4	3	--	2 (1)	-- (--)	1
Apocynaceae	4	3	1	1 (1)	-- (--)	--
Asteraceae	59	30	25	22 (13)	3 (3)	21
Balsaminaceae	1	1	1	-- (--)	1 (0)	--
Boraginaceae	12	4	8	2 (1)	-- (--)	--
Brassicaceae	9	1	8	1 (1)	-- (--)	1
Campanulaceae	1	--	1	1 (1)	-- (--)	1
Cannabaceae	1	1	--	-- (--)	-- (--)	--
Caprifoliaceae	3	2	2	1 (1)	-- (--)	3
Caryophyllaceae	7	1	5	2 (2)	2 (2)	4
Chenopodiaceae	2	2	--	1 (1)	1 (1)	1
Cistaceae	1	--	1	-- (--)	-- (--)	1
Crassulaceae	1	--	--	0	0	1
Cyperaceae	10	7	2	3 (3)	-- (--)	7
Euphorbiaceae	1	1	--	-- (--)	-- (--)	--
Fabaceae	30	23	7	20 (15)	1 (0)	6
Gentianaceae	1	1	--	-- (--)	-- (--)	--

family	total	visible injury	no visible symptoms	growth reduction total (sig.)	growth increase total (sig.)	no growth response
Geraniaceae	3	--	2	-- (--)	-- (--)	2
Hyperaceae	2	2	2	1 (0)	-- (--)	1
Iridaceae	1	--	1	-- (--)	-- (--)	1
Juncaceae	2	--	2	1 (0)	1 (1)	--
Lamiaceae	10	6	5	3 (3)	1 (1)	3
Liliaceae	1	--	1	-- (--)	-- (--)	1
Losaceae	1	1	--	-- (--)	-- (--)	--
Lythraceae	1	--	1	-- (--)	-- (--)	1
Malvaceae	3	2	1	2 (2)	-- (--)	2
Onagraceae	9	9	3	2 (2)	-- (--)	1
Oxalidaceae	1	1		-- (--)	-- (--)	1
Papaveraceae	6	2	3	2 (0)	-- (--)	1
Plantaginaceae	8	2	7	3 (2)	1 (1)	5
Plumbaginaceae	1	--	1	1 (1)	-- (--)	--
Poaceae	60	30	35	26 (17)	6 (3)	37
Polemoniaceae	3	--	3	-- (--)	-- (--)	--
Polygonaceae	11	5	5	5 (5)	2 (1)	4
Primulaceae	1	--	1	-- (--)	-- (--)	1
Ranunculaceae	3	1	3	1 (0)	-- (--)	3
Rosaceae	8	3	5	5 (5)	1 (1)	4
Rubiaceae	2	1	1	1 (0)	-- (--)	1
Saxifragaceae	3	--	3	-- (--)	-- (--)	3
Scrophulariaceae	4	1	2	2 (2)	-- (--)	2
Solanaceae	1	--	1	1 (1)	-- (--)	1
Typhaceae	1	--	1	-- (--)	-- (--)	1
Urticaceae	1	--	1	1 (0)	-- (--)	--
Violaceae	3	2	1	1 (1)	-- (--)	--

The observed trend that about one half of species responded to ozone in a sensitive way is even proved to be valid for species native to Germany including neophytes and archaeophytes (Table 1). About one half of species (198) listed in Annex A, Table 1 are native to Germany representing 4.8 % of German flora (fern and vascular plants). Moreover, 14 species listed are considered to be endangered and additional 14 species are likely to be endangered. Out of these, 16 species (eight within each group) are evidenced to be responsive to ozone (Table 4) Special attention should be paid to the following four species because ozone impacts have been shown for both, growth and leaf injury: *Comarum palustre, Medicago minima*, *Nardus stricta* and *Trifolium striatum* (see also chapter 4.9.1.2 of part I of this report).

Table 4: Species being at risk in Germany (Rote Liste) which have been tested for their response to ozone. If distinct effects have been published, the most sensitive one is listed. n.s. = not significant, -- = not determined.

species	status	injury	growth effect
Antennaria dioica	vulnerable	--	shoot reduction
Avenula pratensis	near-threatened	no	none
Briza media	near-threatened	no	none
Carex laevigata	vulnerable	no	none
Carex panicea	near-threatened	specific	none
Carum carvi	near-threatened	specific	none
Cirsium dissectum	endangered	no	shoot reduction n.s.
Coramrum palustre	near-threatened	yes	growth reduction
Eriophorum vaginatum	near-threatened	--	none
Gentiana asclepiadea	endangered	yes	--
Juncus squarrosus	near-threatened	no	increase in growth
Lychnis flos-cuculi	near-threatened	coloured/specific	none
Lychnis viscaria	near-threatened	no	none
Medicago minima	vulnerable	yes	growth reduction
Micropyrum tenellum	missing/lost	no	--
Nardus stricta	near-threatened	specific	shoot reduction
Narthecium ossifragum	vulnerable	no	none
Primula farinosa	vulnerable	no	none
Rhodiola rosea	extremely rare	--	none
Rubus chamaemorus	endangered	no	--
Salvia pratensis	near-threatened	senescent	none
Saussurea alpina	extremely rare	--	increase
Scrophularia auriculata	vulnerable	no	growth reduction
Senecio sarracenicus	vulnerable	no	increase in shoot
Silene noctiflora	near-threatened	no	none
Succisa pratensis	near-threatened	--	none
Tragopogon orientalis	near-threatened	specific	none
Trifolium striatum	vulnerable	yes	shoot reduction and seed reduction

For references see Annex A.

3.1.2 Evaluation of species’ sensitivity to ozone

In their meta-analyses Hayes et al. (2007) determined an index, to describe the relative sensitivity to ozone for 83 native species from existing publications. “Approximately one-third of the species in their database showed above-ground biomass reductions of about > 10 %”. They concluded that plants of the Fabaceae family and species with a therophyte life form have to be regarded as being particularly sensitive to ozone. Because of its derivation from dose-response curves and its relation to a standardised ozone dose exposure these evidences have to be valued more confident in terms of assessing the relative sensitivity of species.

Nevertheless the main observations of this study comply with the findings when regarding the data set for the 298 species shown in this study (Table 2 and Table 3) although it refers only to the incidence of a sensitive or tolerant response.

Using the database of Hayes et al. (2007) 54 EUNIS (European Nature Information System) level 4 communities were identified as potentially ozone-sensitive with the largest number being associated with grasslands (Mills et al. 2007a). Within the grasslands classification, the communities E4 (alpine and sub-alpine grasslands), E5 (woodland fringes and clearings) and E1 (dry grasslands) have been found to be the most sensitive. In contrast, Bassin et al. (2007a) concluded that species grown in less productive habitats (EUNIS E4 and E1) are thought to be less sensitive than species grown under favorable growth conditions or in productive habitats as mesotrophic pastures. Recently, van Goethem et al. (2013) presented an approach to consider a cumulative stressor-response distribution for ozone exposure on natural vegetation named 'Species Sensitivity Distributions', SSD. Their findings indicate that annual grassland species, as a species assemblage, are more sensitive to ozone than perennial grassland species. The comparison made within the study presented here, may confirm this assumption only for the occurrence of growth effects but not for visible injuries (see Table 2).

3.1.3 Attempts to identify ecological characteristics of ozone susceptibility

When screening plant species according to their relative ozone sensitivity, within the last decades an increasing number of studies aimed on natural or semi-natural herbaceous plant species, and in doing so, European groups focused either on highland or alpine plants (Bungener et al. 1999b; Bungener et al. 1999a), dehesa (Gimeno et al. 2004a), wetland (Franzaring et al. 2000; Batty et al. 2001; Franzaring et al. 2003) or ruderal plants (Bergmann et al. 1999; Bender et al. 2006a). While most of the studies comprised rare species as well, the latter investigated common and widely distributed species, only.

Because it is perfectly obvious that it cannot be our scientific purpose to assess the risk of the total flora of the world by doing standardised screening experiments, here several functional approaches will be discussed to identify ecological characteristics which might be associated with the sensitivity to ozone. Relating eco-physiological characteristics to ozone sensitivity of different species, Harkov & Brennan (1982) concluded that herbaceous species are generally more sensitive than woody plants. In his unifying theory Reich (1987) related the strong dependence of phytotoxic ozone effects to the gas exchange properties of the target plant, thus indicating that water status and transpiration rate might be the critical factor for determining the ozone responsibility of a plant. Franzaring et al. (1997) tested the hypothesis that hygro- and mesomorphous species from moist sites are more affected than scleromorphous species adapted to dry sites. Nevertheless, they failed to evidence a relationship between ozone sensitivity ranking and ELLENBERG-moisture values, especially when based on growth parameters. For their fumigation experiments Franzaring et al. (2000) and Batty et al. (2001) chose wet grassland species which are thought to suffer less water stress in ozone episodes and therefore are considered to be particularly sensitive because of a higher stomatal conductance. In both OTC studies, 36 % of the species responded with growth changes and 56 % expressed symptoms of leaf injury, which exactly reflects the sensitivity of the whole data set shown in this study. Moreover, "there was no association between ecological indicator values for moisture, light, pH and fertility and ozone sensitivity in the short-term experiments" (Batty et al. 2001). However, the most sensitive species in a short-term experiment were characterised by a high stomatal conductance.

In their meta-analyses Hayes et al. (2007) identified three significant relationships between relative sensitivity to ozone and ecological habitat requirements: light, moisture and salt. Further on, these relationships have provided an opportunity to model the relative sensitivity to ozone of species (Jones et al. 2010). In their review on European grasslands, Bassin et al. (2007a) pointed out that three plant traits are main determinants for ozone sensitivity: stomatal conductance, specific leaf area (SLA), and defense capacity.

Low relative growth rate (RGR) and low SLA are characteristic for stress tolerating species (S-strategy sensu CSR strategy modell of Grime (1979) but there is limited evidence that these are less sensitive than species with the highest component of C (competitive)- or R (ruderal)-strategy (Franzaring et al. 1997; Bungener et al. 1999a; Bassin et al. 2007a; Hayes et al. 2007).

However, a basic requirement for deriving any kind of relationship between response to ozone and ecological properties is to embrace a critical number of species covering the broad part of the total ecological amplitude of plants e.g. families, life forms, habitat types, plant traits etc. At present, most of these characteristics were not sufficiently represented in the databases of experiments under realistic conditions (Bassin et al. 2007a; Hayes et al. 2007) narrowing the success in grouping the plant kingdom into broad classes of ozone sensitivity.

3.2 Woody plants

3.2.1 Overview on species investigated and their response to ozone

Out of the huge number of references on the response of woody plants to ozone those have been selected which represent the knowledge sensitivity to ozone in terms of foliar health and growth effects, thus neglecting physiological and biochemical parameters. Therefore, this chapter contains results taken out of 139 references, with 56 of them originated from America, 15 from Asia and 65 from Europe. In summary, a total of 356 records, 164 species, 69 genera and 39 families have been found within the references selected. About two third of the species were categorised as tall trees, and an equal proportion as deciduous. However, only 39 species were native to Germany with 28 more species being neophytes, partly newly invading (Annex A, Table 2). Out of these, *Populus nigra* was the only species being classified as endangered in Germany.

The majority of results have been achieved by using open top chambers (90 studies) and 13 studies used free-air fumigation facilities. Nonetheless, it has to be mentioned, that only six studies presented here investigated mature trees (Havranek & Wieser 1993; Wiltshire et al. 1993; Kelting et al. 1995; Samuelson et al. 1996; Manninen et al. 2003; Nunn et al. 2005) whereas the overwhelming majority of investigations based on experiments with cuttings or seedlings (one to eight years old). Although, currently there is an increasing number of studies using mature trees, these focussed to a greater degree on eco-physiological issues, which are not considered here.

Concerning the parameters registered here, growth parameters were either defined as increases or decreases in growth of whole plants or were specified according to the organs considered. Besides statistically significant changes in plant biomass or the proportion of senescent leaves, effects being not significant but consisting in ≥ 10 % changes are recorded as well and were indicated as “not significant”. The occurrence of visible injuries is indicated as “yes” or “no” or described as increased senescence, if possible. The entire list of data is given in Table 2 (Annex A) and a summary is shown in Table 5 and Table 6. For 64 species both parameters visible injury and growth have been investigated simultaneously. For a majority of more than 70 % (46 species) concordant results had been recorded.

Table 5: Summary of assessments on woody plant species and their responses to ozone given as numbers of total records or species according to different descriptive groups.

	group	visible symptoms			growth effects			
		tested	total (sign.)	none	tested	reduction total (sign.)	increase total (sign.)	none
	total records	**248**	201 (193)	47	**207**	131 (108)	2 (0)	74
	total species	**134**	118 (113)	32	**98**	75 (61)	2 (0)	54
functional type	shrubs	**33**	29 (28)	6	**3**	2 (2)	0	2
	trees	**84**	72 (70)	22	**88**	70 (55)	2 (0)	37
	climbers	**2**	1 (1)	1	**1**	1 (1)	0	0
life history	deciduous	**89**	81 (77)	17	**50**	40 (32)	2 (0)	19
	evergreen	**41**	32 (31)	15	**48**	34 (28)	0	23
leafage	conifers	**18**	14 (13)	8	**30**	19 (16)	0	17
	broadleaved	**117**	104 (100)	24	**68**	56 (45)	2 (0)	25
	native to Germany	**62**	58 (58)	15	**36**	28 (22)	2 (0)	20

Sum of responsive and non-responsive species numbers is not equivalent to the total number of species assessed because of different results within different publications (see Annex A, Table 2).

Table 6: Proportion of responsive species (%) belonging to different descriptive groups. All symptoms and growth responses are combined.

group	injury		growth	
	sign.	total	sign.	total
total records	**77.8**	81.0	**52.2**	63.3
total species	**84.3**	88.1	**62.2**	76.5
shrubs	**84.8**	87.9	**--**	--
trees	**83.3**	85.7	**62.5**	79.5
climbers	**--**	--	**--**	--
deciduous	**86.5**	91.0	**64.0**	80.0
evergreen	**75.6**	78.0	**58.3**	70.8
conifers	**72.2**	77.8	**53.3**	63.3
broadleaved	**85.5**	88.5	**58.8**	70.6
native to Germany	**93.5**	93.5	**61.1**	77.8

If studied repeatedly species may be assessed as both, responsive and not responsive, leading to sums ›100 %.

A total of 146 species showed any response to ozone. In terms of visible leaf injuries more than 80 % of 134 species tested have been estimated to be responsive to ozone. This percentage is slightly higher for deciduous and broadleaved species than for evergreen or coniferous species.

About one half of all observations yielded significant growth responses referring to 62.2 % of a total of 98 species. However, differences between coniferous and broadleaved species are minimal with a slight tendency to more sensitive responses detected for deciduous species. In general, there is no evidence of a significant increase in growth due to elevated ozone. Similarly to herbaceous species, a higher percentage of responsive species was detected when assessing visible leaf injury rather than growth measurements. However, the averaged percentage of responsive woody species is higher than that of herbaceous species (see Table 2).

About 62 % of all woody species (102) have been investigated once, 18 % twice and about 20 % three times and more. The most frequently studied species were *Liriodendron tulipifera, Viburnum lantana, Acer saccharum, Pinus sylvestris, Populus deltoides x nigra, Prunus serotina, Quercus rubra,* and *Betula pendula* (6 to 10 times) *and Pinus taeda, Fraxinus excelsior, Fagus sylvatica,* and *Picea abies* (even more than 10 times).

For a rather small number of species divergent responses have been described in the literature. Although it has to be assumed that within different studies plants of different proveniences have been used and therefore, this apparent disparity in response may be a result of genotypic variation in sensitivity these species are listed below (see chapter 4).

woody species for which divergent responses to ozone are documented (≥ 25 % of studies showed divergent results)

growth: *Eucalyptus globulus*
Larix kaempferi=Larix leptolepis
Cinnamomum camphora
Picea sitchensis
Pinus elliotti
Prunus avium
Pinus sylvestris
Prunus serotina
Quercus rubra
Pinus taeda
Fagus sylvatica
Picea abies

injury: *Corylus avellana*
Olea europaea
Pinus virginiana
Pistacia terebinthus
Cornus sanguinea
Prunus avium
Liriodendron tulipifera
Acer saccharum
Pinus sylvestris
Quercus rubra
Pinus taeda
Picea abies

3.2.2 Evaluation of species' sensitivity to ozone

The data listed in this study (Annex A, Table 2) reflect clearly the fact that our available knowledge about the ozone sensitivity of trees and shrubs derives predominantly from potted juvenile individuals. Karnosky et al. (2007) stated that during more than 50 years of research negative growth effects on forest trees have been demonstrated on seedlings, while ozone response of adult forest trees has rarely been examined experimentally. In order to determine whether seedlings and mature trees responded similarly to ozone, Samuelson & Edwards (1993) exposed 2-yr-old seedlings and 30-yr-old trees of *Quercus rubra* to ozone. Their results indicated that the ozone sensitivity of larger and more physiologically mature trees will be underestimated when represented by young seedlings within exposure experiments.

A first step of a move towards field conditions was made by the use of a free-air exposure facility in a northern temperate forest (AspenFACE, Karnosky et al. 2003b). For old trees, besides some attempts to investigate mature trees by the use of branch cuvettes (Wieser et al. 2012) by now, the free-air ozone exposure system established in a mixed stand of about 60-year-old *Fagus sylvatica* and *Picea abies* trees (Nunn et al. 2002) remains unique.

However, research activities on woody plant species performed within the last decades revealed a broad knowledge on visible symptoms, effects on growth, carbohydrate allocation and detoxification and to a high extent on effects of ozone on photosynthesis and stomatal functioning (e.g. reviewed by Paoletti 2007; Gomez-Garay et al. 2013). These measurements suggested that ozone reduces stomatal conductance and may impair stomatal control and predispose trees to drought stress under dynamic conditions (see chapter 6.1.1). Paoletti (2007) concluded that the most significant ozone impact is on the regulatory capacity of resource allocation rather than on productivity.

As already pointed out for (semi-)natural herbaceous plants species-specific and individual-specific responses to ozone may affect forest competition and biodiversity (Paoletti 2007). Thus, in terms of impacts of ozone on biodiversity issues the knowledge on species' differential sensitivity is important. For example, based on the 38 experiments reviewed by Huttunen & Manninen (2013), *Pinus sylvestris* may be considered as an ozone sensitive conifer species, with mature pines being more sensitive than younger trees. For field-grown mature coniferous trees the higher ozone sensitivity of the deciduous species *Larix decidua* was associated with a higher ozone flux when compared to the evergreen *Picea abies* or *Pinus cembra* (Wieser et al. 2013). In contrast, Schaub et al. (2003) reported on similar ozone uptake rates of two deciduous species (*Prunus serotina* and *Fraxinus americana*) differing in ozone sensitivity as shown by means of visible injury. Also, Zhang et al. (2001) found that there was no correlation between foliar injury and stomatal conductance when comparing 11 deciduous broad leaved trees. The authors suggested that species-specific leaf biochemical processes and environmental interactions must be considered in determining species' sensitivity to ozone. There is evidence that differences in ozone sensitivity can be attributed either to anatomical characteristics (deciduous trees, Bennett et al. 1992) or foliage type specific differences in specific leaf area (evergreen and deciduous conifers Wieser et al. 2013). For example, sclerophyllous Mediterranean species are known to have a high biochemical capacity to cope with oxidative stress and thus are expected to be less sensitive to ozone (Bussotti & Gerosa 2002).

3.3 Agricultural and horticultural crops

A total number of 465 records within 192 references have been found to meet the above mentioned requirements, thus describing the response to ozone of 343 genotypes of 53 crop species (Table 7). Different from other plant groups, screening of crops for ozone sensitivity has started already in the 1950s in USA and the studies referred on here have been performed when the sensitivity of most crop species was known. Thus, apart from some screening studies in Africa or Asia after 1980 mainly sensitive species have been included into experimental studies. As a result, about 90 % of species and 83 % of all cultivars showed a negative growth effect. More than one half of the studies have been performed using OTC exposures, however, recently data on *Glycine max, Oryza sativa, Phaseolus vulgaris, Solanum tuberosum,* and *Triticum aestivum* are also available from free-air fumigation systems (Table 8) The majority of data contained in the list (Annex A, Table 3) derived from European studies but the awareness of air pollution impacts in China and India for example, resulted in a high number of data derived from recently published Asian studies.

Table 7: Summary of growth and injury related information content on agricultural and horticultural crops. Numbers of records, species, and cultivars investigated within studies presented by 192 relevant publications and their response to ozone; concordant response means that leaf injury occurred simultaneously with growth reduction or both were absent.

	total	parameter injury/growth/both	response to ozone					
			injured	not injured	reduced growth/yield	increased growth	no growth response	concordant response
records	465	203 / 401 / 141	179	24	324	4	73	115
species#	53	47 / 46 / 34	42	18	46	3	18	31
cultivars/genotypes*	343	173 / 298 / 117	152	24	246	4	67	95

irrespective of ssp. or var., * except for those, whose response was given as an average exclusively

Table 8: Summary of methods and sites of exposure used in the 192 publications selected to describe growth and injury related responses of agricultural and horticultural crops. (Numbers of records, species, cultivars, and references investigated within studies using different exposure procedures and being realised at different continents).

	exposure facility or method					continent			
	free air	OTC	green-house	controlled environm.	AA + EDU	America	Europe	Asia	Africa
records	43	277	54	76	7	133	165	133	12
species	5[a]	45	14	25	5	20	34	24	9
cultivars	26	218	50	72	6	103	127	100	12
references	13	118	20	31	6	54	129	49	1

[a] these five species are *Glycine max*, *Oryza sativa*, *Phaseolus vulgaris, Solanum tuberosum,* and *Triticum aestivum*

Table 9: List of 53 agricultural and horticultural crop species whose response to ozone has been described by the 192 publications selected. Number of related records and number of various cultivars of a single species which have been investigated.

species	records	cvs	species	records	cvs
Aegilops tauschii	1	1	*Lycopersicon esculentum*	13	9
Allium ampeloprasum	1	1	*Lycopersicon pimpinellifolium*	1	1
Allium cepa	5	5	*Medicago sativa*	5	5
Arachis hypogaea	2	1	*Nicotiana tabacum*	9	9
Avena sativa	1	1	*Oryza sativa*	61	47
Beta vulgaris	4	2	*Phaseolus vulgaris*	62	42
Brassica campestris	11	10	*Pisum sativum*	2	1
Brassica juncea	7	5	*Raphanus sativus*	6	4
Brassica napus ssp oleifera	6	6	*Saccharum spp*	1	1
Brassica oleracea	7	7	*Solanum tuberosum*	11	7
Brassica rapa	4	4	*Spinacia oleracea*	4	4
Cicer arietinum	3	3	*Trifolium alexandrinum*	6	6
Citrullus lanatus	9	7	*Trifolium repens*	5	5
Corchorus olitorius	1	1	*Trigonella foenum-graecum*	1	1
Coriandrum sativum	1	1	*Triticosecale wittmack*	1	1
Cucumis melo	2	2	*Triticum aestivum*	82	48
Cucurbita pepo	3	3	*Triticum boeoticum*	1	1
Daucus carota	3	3	*Triticum dicoccum*	1	1
Eruca sativa	2	2	*Triticum durum*	7	5
Fragaria x ananassa	8	4	*Triticum monococcum*	1	1
Glycine max	53	29	*Triticum polonicum*	1	1
Gossypium barbadense	4	4	*Triticum timopheevii*	1	1
Gossypium hirsutum	8	8	*Valerianella locusta*	3	3
Hordeum vulgare	9	7	*Vicia faba*	1	1
Lactuca sativa	14	11	*Vigna mungo*	1	1
Linum usitatissimum	2	2	*Vigna radiata*	7	7
			Zea mays	5	4

Out of the 53 species considered 16 have only been cited one time, however, among them were old donors of modern wheat cultivars. The most frequently studied species was wheat, followed by bean, rice and soybean (Table 9), each represented by 29 to 48 different cultivars. Related to the literature reviewed here, it could be stated that 75 % of all cultivars and genotypes have been studied once only, 15 % (52 cvs) twice and only 6% (22 cvs) three times. For single cultivars more than three experimental studies have been found: *Lactuca sativa* cv. Paris Island (four times), *Triticum aestivum* cv. Turbo, *Oryza sativa* cv. Koshihikari, and

Solanum tuberosum cv. Bintje (five times), *Glycine max* cv. Essex (seven times) and the snap bean used as biomonitoring plant *Phaseolus vulgaris* cv. Lit even eight times.

As already demonstrated about 90 % of all experiments proved an ozone sensitive response of the cultivars, although for the following cultivars different effects of ozone has been detected:

cultivars for which divergent responses to ozone are documented:

growth: *Brassica campestris* cv. Wisconsin Fast Plants
Fragaria x ananassa cv. Elsanta
Glycine max cv. Essex
Lactuca sativa cv. Paris Island
Lycopersicon esculentum cv. Pusa Ruby
Oryza sativa cvs IR 64, Kasalath, Koshihikari, Nipponbare, Yangdao 6
Phaseolus vulgaris cvs R123, R331, S156
Raphanus sativus cv. Cherry Belle
Solanum tuberosum cv. Bintje
Triticum aestivum cvs Yangfumai 2, Yangmai 15, Yangmai 16, Xannong 19

injury: *Lycopersicon esculentum* cv. Pusa Ruby
Phaseolus vulgaris cv. Bush Blue Lake 274
Triticum aestivum cv. Riband

In order to define sensitivity rankings for cultivars an experimental design is required, which allows to compare the response of different cultivars or genotypes directly. The complete list comprising all 465 records (Annex A, Table 3) put emphasis on cultivar comparison. Referred to the literature considered, 82 studies met these requirements, though, for 28 species data on differential responses of genotypes are available. The number of cultivars per study ranged from 2 (20 species) to 20 (*Oryza sativa*). The majority of genotypes which have been investigated comparatively represent the species *Glycine max, Nicotiana tabacum, Oryza sativa, Phaseolus vulgaris*, and *Triticum aestivum*. For the following 22 species no comparative studies have been found:

22 species for which no studies comparing different cultivars are available:

Aegilops tauschii
Allium ampeloprasum
Arachis hypogaea
Avena sativa
Corchorus olitorius
Coriandrum sativum
Cucurbita pepo
Daucus carota
Eruca sativa
Pisum sativum
Raphanus sativus
Saccharum spp
Solanum tuberosum
Spinacia oleracea
Trigonella foenum-graecum
Triticosecale wittmack
Triticum monococcum
Triticum polonicum
Triticum timopheevii
Valerianella locusta
Vicia faba
Vigna mungo

3.4 Mosses and ferns

There were nine references appropriate to describe the effects of ozone on mosses and ferns involving 21 records of 14 species (Annex A, Table 4). For half of the species growth and length reduction caused by ozone were evidenced (Table 10). The archegoniates regarded here proved to be highly sensitive when considering physiological parameters i.e. membrane permeability or ultrastructure of organelles. However, the data basis is rather small and it remains difficult to assess the risk of mosses and especially of ferns to be impaired by ozone in established ecosystems. Because of its morphological structure stomatal control does not play a role for ozone uptake into mosses and the permanent water film is thought to act as an ozone scavenger (Niemi 2003).

Table 10: Summary of effects of controlled ozone exposures on moss and fern species.

		injury		growth / reproduction		physiological changes	
	total	total no.	injured	total no.	impaired	total no.	impaired
no. of records	21	3	0	10	4	8	7
no. of moss species	12	3	0	6	2	5	5
no. of fern species	2	--	--	2	2	--	--
no. of families	7	2	0	4	4	1	1

3.5 Algae, lichens, and phyllosphere fungi

Most experimental studies on algae have been carried out either with *Chlorella sorokiniana* (Heath et al. 1982; Swanson et al. 1982; Heath 1984) or *Euglena gracilis* (Chevrier et al. 1988; Chevrier et al. 1990; Chevrier & Sarhan 1992; Bilodeau & Chevrier 1998), both grown in bubbled cell cultures. These records all refer to investigations on the mechanisms of ozone-induced oxidative damages and repair at the cellular levels using algae as model cells.

Fenn et al. (1989) examined populations of phyllosphere fungi from leaves of *Sequoiadendron giganteum* and *Quercus kelloggii* exposed to 1.5 x ambient ozone within OTC for 9 to 11 weeks. For none of the tree species total numbers of fungi isolated or the frequency of occurrence of dominant fungi was affected by ozone. However, there was a significant chamber effect since five fungal species had significantly higher isolation frequencies in the open-air treatment compared with those in the treatments within chambers. Magan et al. (1995) analysed the phyllosphere microbial populations inhabiting the needles of conifer species in an open-air fumigation experiment. After three years of exposure to ozone an increase was found in one fungal species each on *Picea sitchensis* and *P. abies* but a decrease in two fungal species (*Epicoccum nigrum* and *Cladosporium* spp) on *Pinus sylvestris*, while total fungal numbers was increased on needles of this species.

Lichens are composites representing a symbiotic union of fungi and algae. Similar to mosses lichens lack mechanisms, such as a waterproofing cuticle and stomata. Lichens are known to be highly responsive to SO_2 (Ahn et al. 2011; Lackovicova et al. 2013) and HNO_3 (Riddell et al. 2012).

There are only a few studies using experimental ozone exposure mainly under controlled environment conditions (8 references see Annex A, Table 5). Besides the observation of visible injuries described by (Ruoss & Vonarburg 1995) physiological and structural impairments have been observed frequently as a result of controlled exposure to high ozone levels (Table

11). Within most studies exposure to ozone was performed under environmental controlled conditions. When using open-top chambers Bertuzzi et al. (2013) concluded, that lichens are actually ozone- tolerant organisms.

Table 11: Summary of effects of controlled ozone exposures on lichens.

	total	no response	ultrastructural changes	visible injury
no. of records	42	19	13	12
no. of species	31	17	13	12

Since several years lichens were frequently utilised as bioindicators for air pollution focusing on photochemical oxidant air pollution in USA (Sigal & Nash 1983; McCune 1988; Will-Wolf et al. 1996; McCune et al. 1997), Scandinavia (Oksanen et al. 1990; Olsson 1995), Switzerland (Ruoss & Vonarburg 1995), Italy (Lorenzini et al. 2003; Nali et al. 2007), Slovenia (Batic & Kralj 1996), and Korea (Hur & Kim 2000; Ahn et al. 2011), for example. However, the lack of a correlation with other ozone response data (Batic & Kralj 1996; Lorenzini et al. 2003) or ozone exposures (Ruoss & Vonarburg 1995; Nali et al. 2007; Ahn et al. 2011) led to the conclusion that lichens distribution seemed not to be suitable for monitoring ozone. Particularly with regard to the fact that the prime activity time of lichens on a daily and a yearly basis did not coincide with periods of high ozone concentrations (Ruoss & Vonarburg 1995). Recently, Pellegrini et al. (2014) investigated the biochemical and physiological mechanisms explaining the high tolerance of lichens to ozone, and found that for the species *Flavoparmelia caperata* high levels of constitutive enzymatic and non-enzymatic defence compounds were formed naturally during the dehydration–rehydration cycles to which lichens are frequently exposed. In terms of ozone the supposition of its suitability was deduced from field observation in the San Bernardino Mountains (see chapter 7.2.5.2).

3.6 Vertebrates

References about responses of vertebrates to controlled ozone exposures found in the literature data bases mainly refer on animal testing associated with medical (pulmonary) research. Very few studies can be classified being related to ecological research; however, these exclusively used acute exposure to high levels of ozone (up to 800 ppb, Annex A, Table 6). The species tested were a guinea pig (*Cavia porcellus,* Su & Gordon 1997), a toad (*Bufo marinus,* Dohm & Mautz 2001; Dohm et al. 2001; Dohm et al. 2008; Johnson et al. 2009), and a frog and a lizard (*Pseudacris cadaverina* and *Sceloporus occidentalis,* Mautz & Dohm 2004). For vertebrates adverse effects on immune function, respiration, hypothermia, and feeding behaviour are described as a result of acute exposures.

One single record was found considering the biodiversity of non-plant species within a field observation: For a Lithuanian forest ecosystem Augustaitis et al. (2007c) described a relationship between peak ozone concentrations and the diversity of small mammals (mainly rodents).

3.7 References

Ahn, C., Chang, E. & Kang, H. W. (2011): Epiphytic macrolichens in Seoul: 35 years after the first lichen study in Korea. Journal of Ecology and Field Biology 34, 381-391.

Augustaitis, A., Augustaitiene, I., Kliucius, A., Mozgeris, G., Pivoras, G., Girgzdiene, R., Arbaciauskas, K., Eitminaviciute, I. & Mazeikyte, R. (2007): Trend in ambient ozone and an attempt to detect its effect on biota in forest ecosystem. Step I of Lithuanian studies. Thescientificworldjournal 7, 37-46.

Bassin, S., Volk, M. & Fuhrer, J. (2007): Factors affecting the ozone sensitivity of temperate European grasslands: An overview. Environmental Pollution 146, 678-691.

Batic, F. & Kralj, A. (1996): Epiphytic lichen vegetation as a biomonitoring system in forest decline studies Slovenia. In: Exceedance of Critical Loads and Levels - Spatial and Temporal Interpretation of Elements in Landscape Sensitivity to Atmospheric Pollutants (ed. by M. Knopflacher, J. Schneider &G. Soja), Wien, pp. 344-353.

Batty, K., Ashmore, M. & Power, S. A. (2001): Assessment of relative sensitivity of wetland plant species to ozone. In: The Ozone Umbrella Project, Centre for Ecology and Hydrology, Edinburgh.

Bender, J., Bergmann, E. & Weigel, H. J. (2006): Responses of biomass production and reproductive development to ozone exposure differ between European wild plant species. Water Air and Soil Pollution 176, 253-267.

Bennett, J. P., Rassat, P., Berrang, P. & Karnosky, D. F. (1992): Relationships between leaf anatomy and ozone sensitivity of Fraxinus-pennsylvanica Marsh. and Prunus-serotina Ehrh. Environmental and Experimental Botany 32, 33-41.

Bergmann, 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.

Bertuzzi, S., Davies, L., Power, S. A. & Tretiach, M. (2013): Why lichens are bad biomonitors of ozone pollution? Ecological Indicators 34, 391-397.

Bilodeau, C. & Chevrier, N. (1998): Endogenous ascorbate level modulates ozone tolerance in Euglena gracilis cells. Plant Physiology and Biochemistry 36, 695-702.

Bungener, P., Nussbaum, S., Grub, A. & Fuhrer, J. (1999a): Growth response of grassland species to ozone in relation to soil moisture condition and plant strategy. New Phytologist 142, 283-293.

Bungener, P., Balls, G. R., Nussbaum, S., Geissmann, M., Grub, A. & Fuhrer, J. (1999b): Leaf injury characteristics of grassland species exposed to ozone in relation to soil moisture condition and vapour pressure deficit. New Phytologist 142, 271-282.

Bussotti, F. & Gerosa, G. (2002): Are the Mediterranean forests in Southern Europe threatened from ozone? Journal of Mediterranean Ecology 3, 23-34.

Chevrier, N. & Sarhan, F. (1992): Effect of ozone on energy metabolism and its relation to carbon dioxide fixation in Euglena gracilis. Journal of Plant Physiology 140, 521-526.

Chevrier, N., Sarhan, F. & Chung, Y. S. (1988): Oxidative damages and repair in Euglena-gracilis exposed to ozone I. Sulfhydryl groups and lipids. Plant and Cell Physiology 29, 321-328.

Chevrier, N., Chung, Y. S. & Sarhan, F. (1990): Oxidative damages and repair in Euglena-gracilis exposed to ozone II. Membrane permeability and uptake of metabolites. Plant and Cell Physiology 31, 987-992.

Dohm, M. R. & Mautz, W. J. (2001): Effects of ozone on marine toad thermoregulatory behavior and immune function. American Zoologist 41, 1429-1429.

Dohm, M. R., Mautz, W. J., Doratt, R. E. & Stevens, J. R. (2008): Ozone exposure affects feeding and locomotor behavior of adult Bufo marinus. Environmental Toxicology and Chemistry 27, 1209-1216.

Dohm, M. R., Mautz, W. J., Looby, P. G., Gellert, K. S. & Andrade, J. A. (2001): Effects of ozone on evaporative water loss and thermoregulatory behavior of marine toads (Bufo marinus). Environmental Research 86, 274-286.

Fenn, M. E., Dunn, P. H. & Durall, D. M. (1989): Effects of ozone and sulfur-dioxide on phyllosphere fungi from 3 tree species. Applied and Environmental Microbiology 55, 412-418.

Franzaring, J., Dueck, T. A. & Tonneijck, A. E. G. (2003): Response of two wet grassland species to ozone and water stress. In: Establishing Ozone Critical Levels II, UNECE Workshop Report. IVL report B 1523 (ed. by P. E. Karlsson, G. Selldén &H. Pleijel), Gothenburg, Sweden pp. 224-229.

Franzaring, J., Bergmann, E., Bender, J. & Weigel, H. J. (1997): The impact of ozone on natural vegetation: An ecological discussion of European studies. In: Proceedings of the Society for Ecology (ed. by J. Pfadenhauer), Gustav Fischer Verlag, Villengang 2, Jena, Germany New York, New York, USA, pp. 355-362.

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

Gimeno, B. S., Bermejo, V., Sanz, J., de la Torre, D. & Elvira, S. (2004): Growth response to ozone of annual species from Mediterranean pastures. Environmental Pollution 132, 297-306.

Gomez-Garay, A., Calderon Guerrero, C., Saiz de Omenaca, J. A. & Manzanera, J. A. (2013): Ozone effects on forests. African Journal of Biotechnology 12, 320-326.

Grime, J. P. (1979): Plant Strategies and Vegetation Processes. Chichester, Wiley.

Harkov, R. S. & Brennan, E. (1982): An ecophysiological analysis of the responses of woody and herbaceous plants to oxidant injury. Journal of Environmental Management 15, 251-261.

Havranek, W. M. & Wieser, G. (1993): Ozone tolerance of European larch (Larix decidua Mill.). Forstwissenschaftliches Centralblatt 112, 56-64.

Hayes, F., Jones, M. L. M., Mills, G. & Ashmore, M. (2007): Meta-analysis of the relative sensitivity of semi-natural vegetation species to ozone. Environmental Pollution 146, 754-762.

Heath, R. L. (1984): Decline in energy reserves of Chorella sorokiniana upon exposure to ozone. Plant Physiology 76, 700-704.

Heath, R. L., Frederick, P. E. & Chimiklis, P. E. (1982): Ozone inhibition of photosynthesis in Chlorella-sorokiniana. Plant Physiology (Rockville) 69, 229-233.

Hur, J. & Kim, P. (2000): Investigation of lichen species as a biomonitor of atmospheric ozone in 'Backwoon' mountain, Korea. Journal of Korean Forestry Society 89, 65-76.

Huttunen, S. & Manninen, S. (2013): A review of ozone responses in Scots pine (Pinus sylvestris). Environmental and Experimental Botany 90, 17-31.

Johnson, S. R., Mautz, W. J. & Dohm, M. R. (2009): Effects of ozone exposure on the specific dynamic action of the cane toad, Bufo marinus. Integrative and Comparative Biology 49, E250-E250.

Jones, M. L. M., Hodges, G. & Mills, G. (2010): Nitrogen mediates above-ground effects of ozone but not below-ground effects in a rhizomatous sedge. Environmental Pollution 158, 559-565.

Karnosky, D. F., Skelly, J. M., Percy, K. E. & Chappelka, A. H. (2007): Perspectives regarding 50 years of research on effects of tropospheric ozone air pollution on US forests. Environmental Pollution 147, 489-506.

Karnosky, D. F., Zak, D. R., Pregitzer, K. S., Awmack, C. S., Bockheim, J. G., Dickson, R. E., Hendrey, G. R., Host, G. E., King, J. S., Kopper, B. J., Kruger, E. L., Kubiske, M. E., Lindroth, R. L., Mattson, W. J., McDonald, E. P., Noormets, A., Oksanen, E., Parsons, W. F. J., Percy, K. E., Podila, G. K., Riemenschneider, D. E., Sharma, P., Thakur, R., Sober, A., Sober, J., Jones, W. S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W. & Isebrands, J. G. (2003): Tropospheric O-3 moderates responses of temperate hardwood forests to elevated CO2: a synthesis of molecular to ecosystem results from the Aspen FACE project. Functional Ecology 17, 289-304.

Kelting, D. L., Burger, J. A. & Edwards, G. S. (1995): The effects of ozone on the root dynamics of seedlings and mature red oak (Quercus rubra L). Forest Ecology and Management 79, 197-206.

Lackovicova, A., Guttova, A., Backor, M., Pisut, P. & Pisut, I. (2013): Response of Evernia prunastri to urban environmental conditions in Central Europe after the decrease of air pollution. Lichenologist 45, 89-100.

Lorenzini, G., Landi, U., Loppi, S. & Nali, C. (2003): Lichen distribution and bioindicator tobacco plants give discordant response: A case study from Italy. Environmental Monitoring and Assessment 82, 243-264.

Magan, N., Kirkwood, I. A., McLeod, A. R. & Smith, M. K. (1995): Effect of open-air fumigation with sulphur dioxide and ozone on phyllosphere and endophytic fungi of conifer needles. Plant Cell and Environment 18, 291-302.

Manninen, S., Sorjamaa, R., Kurki, S., Pirttiniemi, N. & Huttunen, S. (2003): Ozone affects Scots pine phenology and growth. In: Air Pollution, Global Change and Forests in the New Millennium (ed. by D. F. Karnosky, K. E. Percy et al.), pp. 231-246.

Mautz, W. J. & Dohm, M. R. (2004): Respiratory and behavioral effects of ozone on a lizard and a frog. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 139, 371-377.

McCune, B. (1988): Lichen communities along O3 and SO2 gradients in Indianapolis. Bryologist 91, 223-228.

McCune, B., Dey, J., Peck, J., Heiman, K. & WillWolf, S. (1997): Regional gradients in lichen communities of the Southeast United States. Bryologist 100, 145-158.

Mills, G., Hayes, F., Jones, M. L. M. & Cinderby, S. (2007): Identifying ozone-sensitive communities of (semi-)natural vegetation suitable for mapping exceedance of critical levels. Environmental Pollution 146, 736-743.

Nali, C., Balducci, E., Frati, L., Paoli, L., Loppi, S. & Lorenzini, G. (2007): Integrated biomonitoring of air quality with plants and lichens: A case study on ambient ozone from central Italy. Chemosphere 67, 2169-2176.

Nash, T. H., III & Sigal, L. L. (1980): Sensitivity of lichens to air pollution with an emphasis on oxidant air pollutants. General Technical Report, Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, 117-124.

Niemi, R. (2003): Peatland vegetation and carbon gas dynamics under increasing UV-B radiation and ozone concentration. University of Kuopio, Kuopio, Finland.

Nunn, A. J., Reiter, I. M., Haberle, K. H., Langebartels, C., Bahnweg, G., Pretzsch, H., Sandermann, H. & Matyssek, R. (2005): Response patterns in adult forest trees to chronic ozone stress: identification of variations and consistencies. Environmental Pollution 136, 365-369.

Nunn, A. J., Reiter, I. M., Haberle, K. H., Werner, H., Langebartels, C., Sandermann, H., Heerdt, C., Fabian, P. & Matyssek, R. (2002): "Free-air" ozone canopy fumigation in an old-growth mixed forest: Concept and observations in beech. Phyton-Annales Rei Botanicae 42, 105-119.

Oksanen, J., Tynnyrinen, S. & Karenlampi, L. (1990): Testing for increased abundance of epiphytic lichens on a local pollution gradient. Annales Botanici Fennici 27, 301-307.

Olsson, K. (1995): Changes in epiphytic lichen and moss flora in some beech forests in southern Sweden during 15 years. In Ecological Bulletins; Effects of acid deposition and tropospheric ozone on forest ecosystems in Sweden (ed. by H. Staaf &G. Tyler) Copenhagen, pp. 238-247.

Paoletti, E. (2007): Ozone impacts on forests. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2, 13 pp.

Pellegrini, E., Bertuzzi, S., CandottoCarniel, F., Lorenzini, G., Nali, C. & Tretiach, M. (2014): Ozone tolerance in lichens: A possible explanation from biochemical to physiological level using Flavoparmelia caperata as test organism. Journal of Plant Physiology 171, 1514-1523.

Reich, P. B. (1987): Quantifying plant response to ozone: a unifying theory. Tree Physiology 3, 63-91.

Riddell, J., Padgett, P. E. & Nash, T. H. (2012): Physiological responses of lichens to factorial fumigations with nitric acid and ozone. Environmental Pollution 170, 202-210.

Ruoss, E. & Vonarburg, C. (1995): Lichen diversity and ozone impact in rural areas of Central Switzerland. Cryptogamic Botany 5, 252-263.

Samuelson, L. J. & Edwards, G. S. (1993): A comparison of sensitivity to ozone in seedlings and trees of Quercus rubra L. New Phytologist 125, 373-379.

Samuelson, L. J., Kelly, J. M., Mays, P. A. & Edwards, G. S. (1996): Growth and nutrition of Quercus rubra L seedlings and mature trees after three seasons of ozone exposure. Environmental Pollution 91, 317-323.

Schaub, M., Skelly, J. M., Steiner, K. C., Davis, D. D., Pennypacker, S. P., Zhang, J., Ferdinand, J. A., Savage, J. E. & Stevenson, R. E. (2003): Physiological and foliar injury responses of Prunus serotina, Fraxinus americana, and Acer rubrum seedlings to varying soil moisture and ozone. Environmental Pollution 124, 307-320.

Sigal, L. L. & Nash, T. H. (1983): Lichen communities on conifers in Southern-California Mountains - an ecological survey relative to oxidant air-pollution. Ecology 64, 1343-1354.

Su, W. Y. & Gordon, T. (1997): In vivo exposure to ozone produces an increase in a 72-kDa heat shock protein in guinea pigs. Journal of Applied Physiology 83, 707-711.

Swanson, E. S., Toivio-Kinnucan, M., Heath, R. & Cunningham, W. P. (1982): Ozone induces ultrastructural changes in the plama membrane of Chlorella-sorokinana. Plant Cell and Environment 5, 375-384.

van Goethem, T. M. W. J., Azevedo, L. B., van Zelm, R., Hayes, F., Ashmore, M. R. & Huijbregts, M. A. J. (2013): Plant Species Sensitivity Distributions for ozone exposure. Environmental Pollution 178, 1-6.

Wieser, G., Matyssek, R., Gotz, B. & Grünhage, L. (2012): Branch cuvettes as means of ozone risk assessment in adult forest tree crowns: combining experimental and modelling capacities. Trees-Structure and Function 26, 1703-1712.

Wieser, G., Hecke, K., Tausz, M. & Matyssek, R. (2013): Foliage type specific susceptibility to ozone in Picea abies, Pinus cembra and Larix decidua at treeline: A synthesis. Environmental and Experimental Botany 90, 4-11.

Will-Wolf, S., McCune, B., Dey, J. P., Peck, J., Heiman, K., Neitlich, P. & Rosentreter, R. (1996): Air quality assessment in eastern USA forests using regional gradients in lichen communities. Bulletin of the Ecological Society of America 77, 482-482.

Wiltshire, J. J. J., Wright, C. J., Unsworth, M. H. & Craigon, J. (1993): The effects of ozone episodes on autumn leaf fall in apple. New Phytologist 124, 433-437.

Zhang, J., Ferdinand, J. A., Vanderheyden, D. J., Skelly, J. M. & Innes, J. L. (2001): Variation of gas exchange within native plant species of Switzerland and relationships with ozone injury: an open-top experiment. Environmental Pollution 113, 177-185.

4 Intraspecific variation in ozone sensitivity

From its beginning, research on the ozone impact on agricultural and horticultural crops and grassland plant species comprised the assessment of different cultivars and their differential response to this pollutant. When paying more attention to forest trees and wild plant species the variation in ozone sensitivity between populations of different proveniences became an important research objective. Both subjects directly relate to the question about the genetic diversity of crop and wild plant populations and are highly relevant for biodiversity issues in general.

4.1 Importance of breeding activities

In order to maintain crop productivity in a high ozone environment the development and use of ozone tolerant cultivars is suggested to be the most economical and practical solution (Foy et al. 1995; Biswas et al. 2009; Burkey & Carter 2009; Avnery et al. 2013) and the knowledge about the genetic background of ozone sensitivity/tolerance is fundamental for breeding ozone tolerant cultivars (Biswas et al. 2008a).

Experimental studies with the purpose to screen cultivars for their relative sensitivity to ozone have been performed numerously and depending from the set of cultivars tested genotypes of wheat, soybean, snap bean, clover and rice have found to show either differences in their ozone sensitivity or not (see Annex A, Table 3). *Triticum aestivum* is one of the most ozone sensitive crops. Intraspecific variations for modern wheat cultivars have been evidenced by several studies (Reichenauer et al. 1998; Tiwari et al. 2005; Sarkar & Agrawal 2010; Kou et al. 2012; Kou et al. 2013), whereas other cultivars chosen for comparative studies responded similarly to ozone (Barnes et al. 1995; Akhtar et al. 2010; Zhu et al. 2011). With respect to the year of its introduction a screening of old and modern cultivars showed clearly that the more modern the cultivar the greater its sensitivity to ozone (Barnes et al. 1990; Velissariou et al. 1992a; Biswas et al. 2008a; Biswas et al. 2008b). Thus, it may be assumed that inadvertent selection by plant breeders may have resulted in modern cultivars that are more sensitive to ozone than their predecessors (Barnes et al. 1990; Velissariou et al. 1992a).

Measurements of the rate of CO_2 assimilation and stomatal conductance indicate a higher ozone uptake rate in modern cultivars than in older ones (Velissariou et al. 1992a; Biswas et al. 2013). This would suggest that over the years selection for higher yield led to physiological changes e.g. stomatal conductance and thereby inadvertently enhancing the sensitivity to ozone. However, differential responses of wheat cultivars to ozone cannot be explained by differences in ozone-uptake in each instance (Feng et al. 2011b; Inada et al. 2012) and Biswas et al. (2009), for example, concluded that the sensitivity of winter wheat cultivars was related more likely to breeding methods than to ozone concentrations. Although the underlying mechanisms remain unclear, the fact that ozone sensitivity has been changed due to selection by breeders seemed to be certain. Thus, for future breeding activities attention should be paid to the inadvertent loss of the genetic potential for ozone tolerance. Since crop loss due to ozone sensitivity is one aspect of the global climate issue, especially for sensitive crop species the genetic basis of ozone sensitivity needs to be thoroughly studied (Eason & Reinert 1991).

4.2 Evidence for natural selection for ozone tolerance in wild plants

Intact terrestrial ecosystems have the availability to cope with unfavourable and changing environmental conditions with adaptation in accordance with its genotypic capacity. If to our current knowledge exposure to ozone affects growth, vitality, reproductive fitness, and competitive ability of individual plants and provided that these various adverse effects occur either singly or in combination, to a variable extent and in dependence on *i.)* genetic properties, *ii.)* developmental stage, *iii.)* ozone exposure pattern, *iv.)* interaction with other abiotic stressors and/or *v.* biotic stressors ozone pollution is likely to exert a selection process and alter the genetic structure of populations in forest or grassland communities.

Intraspecific differences in ozone tolerance have been evidenced for woody and herbaceous wild plant species, clearly demonstrating that wild genotypes of proximal geographic origin may differ greatly in sensitivity: *Populus tremuloides*, (Karnosky et al. 1992; Karnosky et al. 2003a); *P. tremuloides* x *P. tremula* L., (Oksanen et al. 2001); *Prunus serotina*, (Lee et al. 1999); *Betula pendula*, (Pääkkönen et al. 1993; Pääkkönen et al. 1996; Oksanen 2003); *Pinus densiflora*, (Lee et al. 2006); *Pinus taeda*, (Taylor 1994); *Quercus coccifera* (Elvira et al. 2003); *Anthoxanthum odoratum*, (Dawnay & Mills 2009); *Arabidopsis thaliana*, (Brosche et al. 2010); *Phleum pratense,* (Danielsson et al. 1999) ; *Phleum alpinum*, (Danielsson et al. 1999).

Generally, Giannini & Magnani (1994) stated three different ways by which the genetic structure of a population is affected by environmental conditions: The loss of unfavourable alleles as a result of the death of individuals fitted least or various impacts on reproductive processes directly or indirectly by affecting vegetative processes. Another mechanism which will lead to a change in genotypic composition of a population might consist in an elimination of sensitive individuals by competition (Berrang et al. 1989).

4.2.1 Spatial variations in ozone tolerance

In view of increasing ozone exposure levels and changing diurnal patterns over the last decades it is hypothesised that long-term ozone exposure can increase ozone tolerance of native (plant) species. If so, the genotypic differences of populations of different proveniences exposed to different levels of ozone in the past might be a result of a kind of adaptation that has already occurred. To test this hypothesis in some studies a spatial approach was applied to test whether geographically separated populations of a certain species show differences in their ozone sensitivity/tolerance as a function of the ozone-climate at the corresponding site. The degree of the sensitivity/tolerance of a population was tested experimentally under controlled conditions i.e. exposure to elevated levels of ozone in open-top or environmentally controlled growth chambers.

In the literature, there are some evidences of existing associations between sensitivity and resistance, respectively of a population and ozone climate at different locations (Table 12). Variation in ozone sensitive among different varieties is known for example for *Pinus strobus, Populus tremuloides,* and *Acer rubrum*. The finding that ozone and/or pollutant sensitive genotypes are under-represented within populations in eastern North America is interpreted to indicate Stage I of natural selection: the elimination of sensitive genotypes, which was attributed to the impact of ozone and/or other regional air pollutants (Karnosky et al. 1989a; Karnosky et al. 1989b; Berrang et al. 1991). However, it remains uncertain whether together with sensitive genotypes useful rare alleles that would be beneficial in the future are lost (Karnosky et al. 1989b). Loss of a significant portion of the germplasm in natural forest ecosystems must be considered a significant problem, particularly if some genes are found exclusively in the sensitive genotypes as suggested by isozyme studies of *Picea abies* clones (Karnosky et al. 1989a).

The most prominent example for the observation of spatial variation in ozone resistance is given by the wild plant *Plantago major*. Estimating the relative ozone resistance of 28 geographically separated populations, which had been collected all over UK, a British group succeeded in demonstrating that the differential ozone resistance was statistically related primarily to the ozone climate of its site of origin (Reiling & Davison 1992; Pearson et al. 1996; Lyons et al. 1997). A positive relationship was found between the relative ozone resistance and descriptors of the ozone-climate at the site of seed collection for the year of, and the second year before seed collection (Lyons et al. 1997). However, the relative responses of the populations varied according to the ozone treatment (Pearson et al. 1996).

In some studies, intraspecific differences in ozone tolerance between populations originating from different proveniences are shown, but a correlation with the ozone climate was difficult to fit (Table 13). This partly could be explained by a high variability within the populations (Kline et al. 2009). For *P. tremuloides* Berrang et al. (1986) found differences in ozone sensitivity among clones within populations being larger than differences among populations. Furthermore, Berrang et al. (1991) identified two climatic variables, annual precipitation and minimum temperature, which correlate with the amount of leaf injuries as well.

Table 12: Evidence of spatial variations in ozone resistance.

species	**study area**	**no.**	**experimental set up**	**Reference**
Plantago major	UK	28	controlled, 70 ppb, 2wk	(Reiling & Davison 1992)
Plantago major	Europe (ICP-Crops)	20	controlled, 70 ppb, 2wk	(Lyons et al. 1997)
Trifolium campestre	Switzerland, north / south	2	OTC, AA, AA+	(Fuhrer et al. 1998)
Phleum pratense	Scandinavia	9	OTC, CF+70 ppb, NF+50 ppb	(Danielsson et al. 1999)
Populus tremuloides	USA, eastern national parks	5	GH, 180 ppb, 6h	(Berrang et al. 1986)
	USA, national parks	15	GH, 150 ppb, 6h	(Berrang et al. 1991)
	USA, New York, Michigan	5	AA	(Berrang et al. 1989)
	USA, Great Lakes region	6	AA	(Karnosky et al. 2003a)

no. = number of populations or sites considered

Table 13: Indication of spatial differences in ozone resistance without statistical significance.

species	**study area**	**no.**	**experimental set up**	**Reference**
Trifolium repens *Trifolium pratense*	Switzerland	???	100 ppb, 6 d 150 ppb, 3 d	(Nebel & Fuhrer 1994)
Phleum pratense	Scandinavia	9	OTC, CF+70 ppb, NF+50 ppb	(Danielsson et al. 1999)
Epilobium hirsutum	UK	18		(Davison & Haley 2001).
Asclepias syriaca	midwestern USA	9	GH, 40 to 80 ppb	(Kline et al. 2009)
Apocynum cannabinum	midwestern USA	16	GH, 40 to 80 ppb	(Kline et al. 2009)
Prunus serotina	USA, Pennsylvania, West Virginia	15	AA	(Lee et al. 1999)
Betula pubescens	Scandinavia	5	GH, 20 to 116 ppb	(Mortensen 1998)

no. = number of populations or sites considered

4.2.2 Genetic aspects of spatial variation in ozone tolerance

Environmental stress is acknowledged to affect the genetic structure of populations in different ways (Staszak et al. 2007). Evidence for changes in genetic variation due to air pollution was already given by Bergmann & Scholz (1989) and Ruetz & Bergmann (1989): For some gene loci a comparison between healthy and damaged *Picea abies* trees showed differences in heterozygosity with certain heterozygotes occur more frequently among the healthy trees. More recently, a similar relationship was found for *Pinus ponderosa* with ozone tolerant trees being more heterozygous than ozone sensitive individuals (Staszak et al. 2004). Moreover, differences in signatures of genetic structure between saplings and mature trees in *P. ponderosa* and *P. jeffrey* suggest that an increase in pollution over the last 50 years, and episodic drought stress may have affected the genetic structure of two pine species in Sequoia National Park (Staszak et al. 2007).

Wolff et al. (2000) analysed genetic markers associated with ozone resistance in *P. major* and expanded the study area to 27 continental European sites. They found that gaining tolerance to ozone was associated with a decrease in genetic variation over time. Because the genetic composition showed no drastic changes it was assumed that the change in tolerance to ozone was probably the result of selection on genotypes already present in local populations (selection *in situ*). In addition, their finding revealed that selection for ozone tolerance may involve a number of genetically determined traits and thus conclude that plants with similar degrees of ozone tolerance are not closely related (Wolff et al. 2000).

Bassin et al. (2004) examined the genetic distinctiveness of the five *Centaurea jacea* populations originating from different European countries (Norway, Hungary, Switzerland, Italy, Slovenia) showing a high degree of intra-specific variability in ozone sensitivity. Their results indicate a qualitative relationship between population genetic divergence and variability in ozone sensitivity. As shown by DNA fingerprinting assays populations of *Rudbeckia laciniata* sampled at different sites in the Great Smoky Mountains National Park, USA, differ in genetic diversity, on the other hand, symptoms may vary greatly within a single genet (Davison et al. 2003).

4.2.3 Temporal changes in ozone tolerance

In addition to spatial variations of *Plantago major* a temporal change in ozone resistance over a short period of time was reported. For two populations an increase in ozone resistance after summers when ozone concentrations were high has been proved (Davison & Reiling 1995; Whitfield et al. 1997). Irrespective of a change in ozone resistance, Kolliker et al. (2008) recently demonstrated that differences in genetic composition and diversity are detectable in populations of the species *Plantago lanceolata* after exposure of an old semi-natural grassland to elevated ozone for five years.

Heagle et al. (1991) propagated *Trifolium repens* plants clonally that survived after exposure to different levels of ozone under inter- and intra-specific field conditions. After two years clones sampled from the high ozone plots exhibited a higher percentage of ozone tolerant clones than those treated with low ozone. Both studies indicate that ozone stress might represent a selection pressure for tolerance to ozone.

In contrast, repeated exposure for six years of trees led to an increase in sensitivity in trees (*Betula pendula*), which partly was explained by a change in growth form and deleterious carry-over effects (Oksanen 2003).

4.2.4 Conclusion

The inheritance of ozone resistance as known from crops (Mebrahtu et al. 1990; Heggestad 1991; Burkey & Carter 2009) even has been demonstrated for wild plant species (Whitfield et al. 1997; Lee et al. 2002). Provided that genotypes may vary greatly in ozone sensitivity natural and semi-natural plant populations offer a potential for natural selection for ozone tolerance. In fact, there is evidence that micro-evolutionary processes could take place in response to long-term elevated ozone exposure and at some regions ambient ozone levels are sufficiently high to promote this evolution (Berrang et al. 1986; Berrang et al. 1991; Lyons et al. 1997; Kolliker et al. 2008). Germplasm loss and the subsequent decrease in genetic diversity could be a more important air pollution impact in the long run than short-term economic losses (Karnosky et al. 1989a).

Moreover, a decrease in genetic variation has been proved over time (Wolff et al. 2000). With respect to future climate and environmental conditions, this reduction of genetic diversity would have profound implications as it may reduce the plasticity of the population in a changing environment.

4.3 References

Akhtar, N., Yamaguchi, M., Inada, H., Hoshino, D., Kondo, T., Fukami, M., Funada, R. & Izuta, T. (2010): Effects of ozone on growth, yield and leaf gas exchange rates of four Bangladeshi cultivars of rice (Oryza sativa L.). Environmental Pollution 158, 2970-2976.

Avnery, S., Mauzerall, D. L. & Fiore, A. M. (2013): Increasing global agricultural production by reducing ozone damages via methane emission controls and ozone-resistant cultivar selection. Global Change Biology 19, 1285-1299.

Barnes, J. D., Ollerenshaw, J. H. & Whitfield, C. P. (1995): Effects of elevated CO2 and/or O3 on growth, development and physiology of wheat (Triticum aestivum L.). Global Change Biology 1, 129-142.

Barnes, J. D., Velissariou, D., Davison, A. W. & Holevas, C. D. (1990): Comparative ozone sensitivity of old and modern Greek cultivars of spring wheat. New Phytologist 116, 707-714.

Bassin, S., Kolliker, R., Cretton, C., Bertossa, M., Widmer, F., Bungener, P. & Fuhrer, J. (2004): Intra-specific variability of ozone sensitivity in Centaurea jacea L., a potential bioindicator for elevated ozone concentrations. Environmental Pollution 131, 1-12.

Bergmann, F. & Scholz, F. (1989): Selection effects of air pollution in Norway spruce (Picea abies) populations. In: Genetic Effects of Air Pollutants in Forest Tree Populations (ed. by F. Scholz, H.-R. Gregorius &D. Rudin), Springer Berlin Heidelberg, pp. 143-160.

Berrang, P., Karnosky, D. F. & Bennett, J. P. (1989): Natural Selection for Ozone Tolerance in Populus tremuloides: Field Verification. Canadian Journal of Forest Research 19, 519-522.

Berrang, P., Karnosky, D. F. & Bennett, J. P. (1991): Natural-selection for ozone tolerance in Populus tremuloides - an evaluation of nationwide trends. Canadian Journal of Forest Research 21, 1091-1097.

Berrang, P., Karnosky, D. F., Mickler, R. A. & Bennett, J. P. (1986): Natural-selection for ozone tolerance in Populus tremuloides Canadian Journal of Forest Research 16, 1214-1216.

Biswas, D. K., Xu, H., Li, Y. G., Ma, B. L. & Jiang, G. M. (2013): Modification of photosynthesis and growth responses to elevated CO2 by ozone in two cultivars of winter wheat with different years of release. Journal of Experimental Botany 64, 1485-1496.

Biswas, D. K., Xu, H., Li, Y. G., Liu, M. Z., Chen, Y. H., Sun, J. Z. & Jiang, G. M. (2008a): Assessing the genetic relatedness of higher ozone sensitivity of modern wheat to its wild and cultivated progenitors/relatives. Journal of Experimental Botany 59, 951-963.

Biswas, D. K., Xu, H., Li, Y. G., Sun, J. Z., Wang, X. Z., Han, X. G. & Jiang, G. M. (2008b): 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.

Biswas, D. K., Xu, H., Yang, J. C., Li, Y. G., Chen, S. B., Jiang, C. D., Li, W. D., Ma, K. P., Adhikary, S. K., Wang, X. Z. & Jiang, G. M. (2009): Impacts of methods and sites of plant breeding on ozone sensitivity in winter wheat cultivars. Agriculture Ecosystems & Environment 134, 168-177.

Brosche, M., Merilo, E., Mayer, F., Pechter, P., Puzorjova, I., Brader, G., Kangasjarvi, J. & Kollist, H. (2010): Natural variation in ozone sensitivity among Arabidopsis thaliana accessions and its relation to stomatal conductance. Plant Cell and Environment 33, 914-925.

Burkey, K. O. & Carter, T. E. (2009): Foliar resistance to ozone injury in the genetic base of US and Canadian soybean and prediction of resistance in descendent cultivars using coefficient of parentage. Field Crops Research 111, 207-217.

Danielsson, H., Gelang, J. & Pleijel, H. (1999): Ozone sensitivity, growth and flower development in Phleum genotypes of different geographic origin in the Nordic countries. Environmental and Experimental Botany 42, 41-49.

Davison, A. W. & Reiling, K. (1995): A rapid change in ozone resistance of Plantago major after summers with high ozone concentrations. New Phytologist 131, 337-344.

Davison, A. W. & Haley, H. (2001): Assessment of relative sensitivity of wetland plant species to ozone. In: The Ozone Umbrella Project, Centre for Ecology and Hydrology, Edinburgh.

Davison, A. W., Neufeld, H. S., Chappelka, A. H., Wolff, K. & Finkelstein, P. L. (2003): Interpreting spatial variation in ozone symptoms shown by cutleaf cone flower, Rudbeckia laciniata L. Environmental Pollution 125, 61-70.

Dawnay, L. & Mills, G. (2009): Relative effects of elevated background ozone concentrations and peak episodes on senescence and above-ground growth in four populations of Anthoxanthum odoratum L. Environmental Pollution 157, 503-510.

Eason, G. & Reinert, R. A. (1991): Responses of closely related bush blue lake snap bean cultivars to increasing concentrations of ozone. Journal of the American Society for Horticultural Science 116, 520-524.

Elvira, S., Bermejo, V., Manrique, E. & Gimeno, B. S. (2003): Differential response of two Quercus coccifera populations to their long-term ozone exposure. In: Establishing Ozone Critical Levels II, UNECE Workshop Report. IVL report B 1523 (ed. by P. E. Karlsson, G.Selldén &H. Pleijel), Gothenburg, Sweden pp. 363-368.

Feng, Z. Z., Pang, J., Kobayashi, K., Zhu, J. G. & Ort, D. R. (2011): Differential responses in two varieties of winter wheat to elevated ozone concentration under fully open-air field conditions. Global Change Biology 17, 580-591.

Foy, C. D., Lee, E. H., Rowland, R., Devine, T. E. & Buzzell, R. I. (1995): Ozone tolerance related to flavonol glycoside genes in soybean. Journal of Plant Nutrition 18, 637-647.

Fuhrer, J., Endtner, V., Bungener, P., Nussbaum, S. & Grub, A. (1998): Intraspecific differences in ozone tolerance.

Giannini, R. & Magnani, F. (1994): Impact of global change on pollination processes and on the genetic diversity of forest tree populations. Forest Genetics 1, 97-104.

Heagle, A. S., McLaughlin, M. R., Miller, J. E., Joyner, R. L. & Spruill, S. E. (1991): Adaptation of a white clover population to ozone stress. New Phytologist 119, 61-68.

Heggestad, H. E. (1991): Origin of Bel W3, Bel C and Bel B tobacco varieties and their use as indicators of ozone. Environmental Pollution 74, 264-291.

Inada, H., Kondo, T., Akhtar, N., Hoshino, D., Yamaguchi, M. & Izuta, T. (2012): Relationship between cultivar difference in the sensitivity of net photosynthesis to ozone and reactive oxygen species scavenging system in Japanese winter wheat (Triticum aestivum). Physiologia Plantarum 146, 217-227.

Karnosky, D. F., Berrang, P. C., Scholz, F. & Bennett, J. P. (1989): Variation in and natural selection for air pollution tolerances in trees. In: Genetic Effects of Air Pollutants in Forest Tree Populations - Proceedings of the Joint Meeting of the IUFRO Working Parties Genetic Aspects of Air Pollution Population and Ecological Genetics Biochemical Genetics held in Großhansdorf, August 3–7, 1987 (ed. by F. Scholz, H. R. Gregorius &D. Rudin), Springer, Berlin, Heidelberg, pp. 29-38.

Karnosky, D. F., Scholz, F., Geburek, T. & Rudin, D. (1989): Implications of genetic effects of air pollution on forest ecosystems knowledge gaps. In: Genetic Effects of Air Pollutants in Forest Tree Populations - Proceedings of the Joint Meeting of the IUFRO Working Parties Genetic Aspects of Air Pollution Population and Ecological Genetics Biochemical Genetics held in Großhansdorf, August 3–7, 1987 (ed. by F. Scholz, H. R. Gregorius &D. Rudin), Springer, Berlin, Heidelberg, pp. 199-201.

Karnosky, D. F., Gagnon, Z. E., Reed, D. D. & Witter, J. A. (1992): Growth and biomass allocation of symptomatic and asymptomatic Populus tremuloides clones in response to seasonal ozone exposures. Canadian Journal of Forest Research 22, 1785-1788.

Karnosky, D. F., Percy, K. E., Mankovska, B., Prichard, T., Noormets, A., Dickson, R. E., Jepsen, E. & Isebrands, J. G. (2003): Ozone affects the fitness of trembling aspen. In: Air Pollution, Global Change and Forests in the New Millennium (ed. by D. F. Karnosky, K. E. Percy et al.), Elsevier, pp. 199-209.

Kline, L. J., Davis, D. D., Skelly, J. M. & Decoteau, D. R. (2009): Variation in ozone sensitivity within indian hemp and common milkweed selections from the Midwest. Northeastern Naturalist 16, 307-313.

Kolliker, R., Bassin, S., Schneider, D., Widmer, F. & Fuhrer, J. (2008): Elevated ozone affects the genetic composition of Plantago lanceolata L. populations. Environmental Pollution 152, 380-386.

Kou, T.-J., Yu, W.-W., Zhu, J.-G. & Zhu, X.-K. (2012): Effects of ozone pollution on the accumulation and distribution of dry matter and biomass carbon of different varieties of wheat. Huanjing Kexue 33, 2862-2867.

Kou, T., Yu, W., Liu, D., Zhu, J. G. & Zhu, X. K. (2013): Effects of elevated ozone on absorption and distribution of nutrients in different cultivars of wheat. Acta Scientiae Circumstantiae 33, 644-649.

Lee, J. C., Oh, C. Y. & Han, S. H. (2006): Foliar injury, growth, and SOD activity of Pinus densiflora exposed to ozone. In: Air Pollution XIV (ed. by J. W. S. Longhurst &C. A. Brebbia), pp. 575-584.

Lee, J. C., Steiner, K. C., Zhang, J. W. & Skelly, J. M. (2002): Heritability of ozone sensitivity in open-pollinated families of black cherry (Prunus serotina Ehrh.). Forest Science 48, 111-117.

Lee, J. C., Skelly, J. M., Steiner, K. C., Zhang, J. W. & Savage, J. E. (1999): Foliar response of black cherry (Prunus serotina) clones to ambient ozone exposure in central Pennsylvania. Environmental Pollution 105, 325-331.

Lyons, T. M., Barnes, J. D. & Davison, A. W. (1997): Relationships between ozone resistance and climate in European populations of Plantago major. New Phytologist 136, 503-510.

Mebrahtu, T., Mersie, W. & Rangappa, M. (1990): Inheritance of ambient ozone insensitivity in common bean (Phaseolus vulgaris L.). Environmental Pollution 67, 79-89.

Mortensen, L. M. (1998): Growth responses of seedlings of six Betula pubescens Ehrh. provenances to six ozone exposure regimes. Scandinavian Journal of Forest Research 13, 189-196.

Nebel, B. & Fuhrer, J. (1994): Interspecific and intraspecific differences in ozone sensitivity in seminatural plant-communities. Angewandte Botanik 68, 116-121.

Oksanen, E. (2003): Responses of selected birch (Betula pendula Roth) clones to ozone change over time. Plant Cell and Environment 26, 875-886.

Oksanen, E., Amores, G., Kokko, H., Santamaria, J. M. & Kärenlampi, L. (2001): Genotypic variation in growth and physiological responses of Finnish hybrid aspen (Populus tremuloides x P-tremula) to elevated tropospheric ozone concentration. Tree Physiology 21, 1171-1181.

Pääkkönen, E., Paasisalo, S., Holopainen, T. & Karenlampi, L. (1993): Growth and stomatal responses of birch (Betula pendula Roth) clones to ozone in open-air and chamber fumigations. New Phytologist 125, 615-623.

Pääkkönen, E., Vahala, J., Holopainen, T., Karjalainen, R. & Kärenlampi, L. (1996): Growth responses and related biochemical and ultrastructural changes of the photosynthetic apparatus in birch (Betula pendula) saplings exposed to low concentrations of ozone. Tree Physiology 16, 597-605.

Pearson, S., Davison, A. W., Reiling, K., Ashenden, T. & Ollerenshaw, J. H. (1996): The effects of different ozone exposures on three contrasting populations of Plantago major. New Phytologist 132, 493-502.

Reichenauer, T. G., Goodman, B. A., Kostecki, P. & Soja, G. (1998): Ozone sensitivity in Triticum durum and T-aestivum with respect to leaf injury, photosynthetic activity and free radical content. Physiologia Plantarum 104, 681-686.

Reiling, K. & Davison, A. W. (1992): Spatial variation in ozone resistance of British populations of Plantago major L. New Phytologist 122, 699-708.

Ruetz, W. F. & Bergmann, F. (1989): Möglichkeiten zum Nachweis von autochthonen Hochlagenbeständen der Fichte (Picea abies) in den Berchtesgadener Alpen. Forstwissenschaftliches Centralblatt 108, 164-174.

Sarkar, A. & Agrawal, S. B. (2010): Elevated ozone and two modern wheat cultivars: An assessment of dose dependent sensitivity with respect to growth, reproductive and yield parameters. Environmental and Experimental Botany 69, 328-337.

Staszak, J., Grulke, N. E. & Prus-Glowacki, W. (2004): Genetic differences of Pinus ponderosa Dougl. ex Laws. trees tolerant and sensitive to ozone. Water Air and Soil Pollution 153, 3-14.

Staszak, J., Grulke, N. E., Marrett, M. J. & Prus-Glowacki, W. (2007): Isozyme markers associated with O-3 tolerance indicate shift in genetic structure of ponderosa and Jeffrey pine in Sequoia National Park, California. Environmental Pollution 149, 366-375.

Taylor, G. E. (1994): Plant and environment interaction: role of genotype in the response of loblolly pine to tropospheric ozone - Effects at the whole-tree, stand, and regional level. Journal of Environmental Quality 23, 63-82.

Tiwari, S., Agrawal, M. & Manning, W. J. (2005): Assessing the impact of ambient ozone on growth and productivity of two cultivars of wheat in India using three rates of application of ethylenediurea (EDU). Environmental Pollution 138, 153-160.

Velissariou, D., Barnes, J. D. & Davison, A. W. (1992): Has inadvertent selection by plant breeders affected the O3 sensitivity of modern Greek cultivars of spring wheat. Agriculture Ecosystems & Environment 38, 79-89.

Whitfield, C. P., Davison, A. W. & Ashenden, T. W. (1997): Artificial selection and heritability of ozone resistance in two populations of Plantago major. New Phytologist 137, 645-655.

Wolff, K., Morgan-Richards, M. & Davison, A. W. (2000): Patterns of molecular genetic variation in Plantago major and P-intermedia in relation to ozone resistance. New Phytologist 145, 501-509.

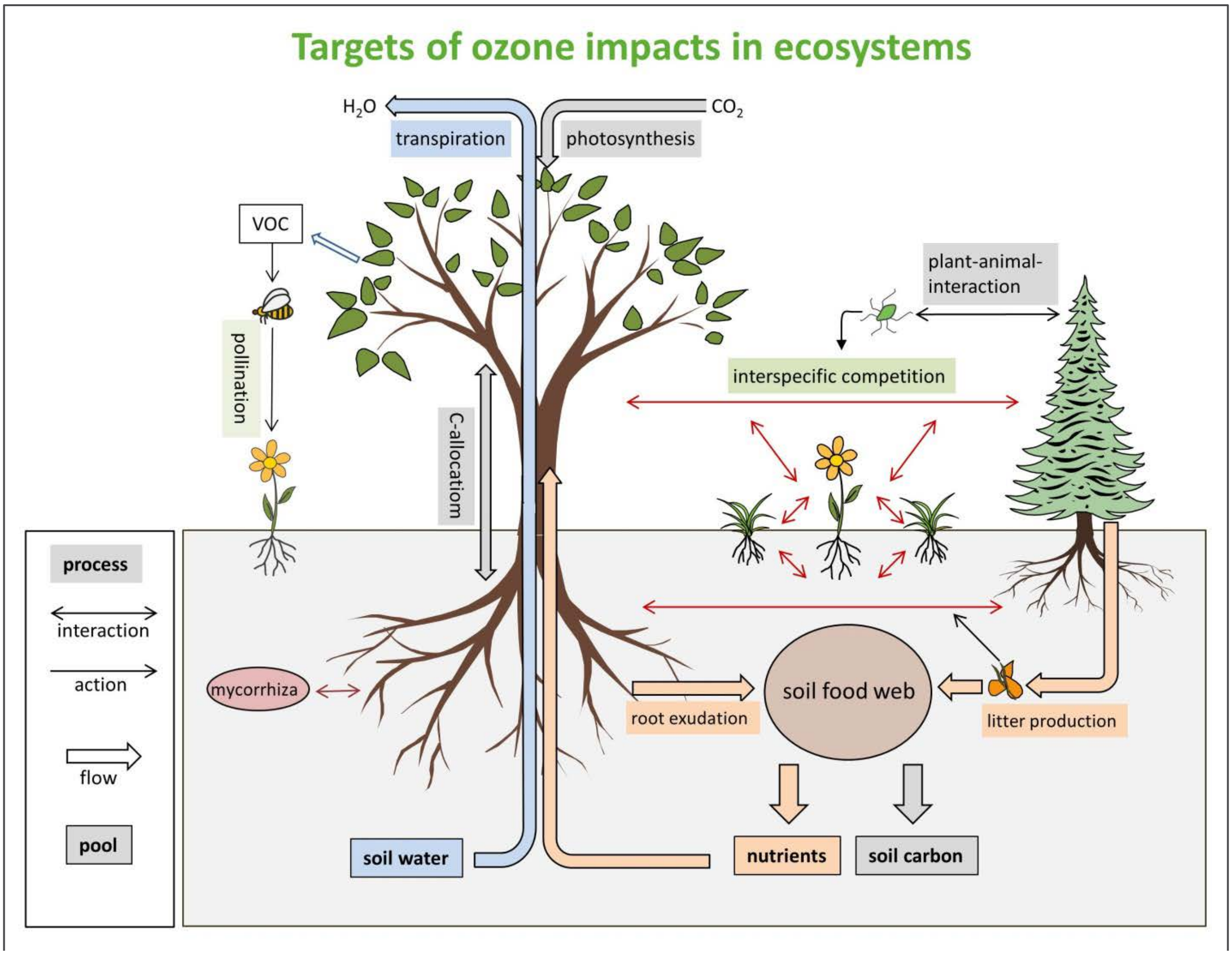
Zhu, X. K., Feng, Z. Z., Sun, T. F., Liu, X. C., Tang, H. Y., Zhu, J. G., Guo, W. S. & Kobayashi, K. (2011): Effects of elevated ozone concentration on yield of four Chinese cultivars of winter wheat under fully open-air field conditions. Global Change Biology 17, 2697-2706.

5 Effects of ozone on biotic interactions

In ecosystems, there are complex interactions between plants and other biotic factors, which are known to be subjected to the impact of ozone. This impact may become apparent either in modifying ozone effects by the presence of biotic interactions or ozone itself may modify plant responses to interacting biotic factors. Thus, there are numerous organisms and processes, which are affected by ozone indirectly i.e. mediated by the response of a susceptible receptor, the plant. This chapter is aimed to report on the current knowledge of the susceptibility to ozone of biotic interactions in ecosystems with plants occupying a central position and will encompass inter- and intra-specific plant competition, interaction with herbivores, pathogen and beneficial microbes, as well as all kinds of soil organisms (Figure 1).

The studies cited here had been selected to contribute to the answer of the central question, whether ozone at ambient or elevated levels have the ability to alter the structure or composition of communities of either plants, microbes, arthropods or insects mediated by plants.

Figure 1: Organisms, processes, and pools affected by ozone within an ecosystem.



Plant competition, plant-animal interaction, soil-born organisms and belowgroung processes are described in this chapter, ozone effects on VOC emission, primary production, transpiartion, and soil water / soil carbon will follow in chapter 6.

5.1 Plant competition and community composition

In a field study conducted in southern California, the expression of ozone foliar injury on ponderosa pine depended on the distance to the nearest conspecific individual (Grulke & Lee 1997). This example may demonstrate in a simple way the importance of regarding an ecosystem in its entirety.

In any plant community its constituting individuals compete with one-another for light, water, and nutrients and competition is an important factor driving the development of plant populations. As plant growth responses to ozone significantly vary between species and genotypes (see chapter 3 and 4), the obvious question/assumption is whether exposure to high levels of ozone may alter the strength of competitive interactions for soil resources. Thus, elevated ozone is thought to have the potential to cause a change in the relative composition of mixed stands. Previous studies suggested that poor competitors have an added disadvantage in elevated ozone (Kubiske et al. 2007). The way by which elevated levels of ozone will shape the composition includes a change in the cover or abundance of plant species, which in turn will change its genetic structure.

Currently, the urgent challenge to describe ozone risks to communities is the understanding of how competitive interactions will modify growth responses of individual components to ozone and, conversely, how the impact of ozone will modify their competitive ability within a plant assemblage.

In the following, about 80 publications describing experiments on ozone effects on plant competition will be presented involving both, old established ecosystems and newly created plant communities. The main part of experimental studies (this chapter includes about 70 references) was designed to study effects of ozone on competition in artificial two-species mixtures or model plant communities under laboratory or field conditions. With few exceptions this research activities can be grouped according to land use practices into grassland, forest and agro-ecosystem. For grassland communities the use of field exposure chambers, such as open top chambers and solardomes, was proved to be suitable, whereas for studies on forest communities, chamberless exposure technics were used more frequently, especially in the course of the Aspen FACE project (see chapter 5.1.2.3). Beside case studies in the field (see chapter 7) manipulative experiments on established communities and ecosystems are judged to rank high at the scale of ecologically relevance and hierarchical level. Here, state of knowledge and most important findings about response to ozone of competition in grassland and forest ecosystem obtained by manipulating ozone exposure is compiled.

5.1.1 Grassland

5.1.1.1 Established communities of managed and semi-natural grassland

The first effort to study complex plant communities was done by Nebel & Fuhrer (1994), who exposed soil blocks with intact semi-natural grassland vegetation from different sites in Switzerland to elevated ozone under climate-controlled conditions. Thus, 31 species were classified according to the appearance of visible injury when grown in competition. Later on, different experimental designs were adapted to this issue including the transplantation of monoliths from the field into fumigation chambers, the use of open top chambers and of chamberless fumigation facilities in established pastures (see Annex C, Table 7).

To our knowledge there was only one single study assessing the effect of ambient ozone pollution on a **field grown established semi-natural grassland** by the use of charcoal filtered air in OTCs. Evans & Ashmore (1992) showed that during a season with relative high ozone levels (41 ppb, 7h mean) total above-ground biomass was decreased in non-filtered air relative to CF. However, in contrast to expectations from screening experiments this decrease was confined to the major grass species *Agrostis capillaris* whereas the forb species (dominated by *Trifolium repens* and *Veronica chamaedrys*) showed an increase in biomass.

In Switzerland, in 1999 a novel free-air fumigation system was designed to investigate effects of ozone exposure on a species-rich (53 species) old pasture at a mid-elevation site under real field conditions. There was no difference in microclimatic conditions between experimental plots and ambient conditions (Volk et al. 2003). For single growth periods, no relationship between ozone exposure level and yield differences between treatments was observed. After five years of this field experiment, a loss in annual dry matter yield of about 23 % was detected in moderately elevated ozone (1.5 x ambient air) showing a strong negative response of the yield of the fraction of legumes (Volk et al. 2006) but not in the frequency sum of legumes (Stampfli & Fuhrer 2010). The main ozone effect could be described as a temporal change in sward composition from an initial prevalence of forbs in ozone plots and a prevalence of grasses in control plots towards a balanced ratio in both treatments. In their re-analysis Stampfli & Fuhrer (2010) put emphasize on the sward's productivity prior to the start of fumigation and concluded that spatial heterogeneity in pre-treatment nutrient status did not allow to relate temporal changes in total yield and yield of legumes to ozone. Thus, they concluded that species-rich mature grassland (47 species) such as the one studied at 'Le Mouret' may be less sensitive to elevated ozone than previously assumed.

A second experiment based on free air exposures was conducted in UK and consisted in three experimental transects to produce concentration gradients over upland mesotrophic grassland (Wedlich et al. 2012). Exposure to ozone elevated by mean concentrations of up to 10 ppb significantly decreased herb biomass, but not total grass or legume biomass in the second and the third year. In contrast to Stampfli & Fuhrer (2010) this study revealed a clear evidence of accumulative effect of ozone over time on species biomass composition.

Mostly, in experiments with **transplanted grassland swards** low managed and low productivity grasslands have been investigated showing that exposure to elevated ozone did not affect the total biomass (calcareous grassland UK, Thwaites et al. 2006 and subalpine grassland, Volk et al. 2011, see Annex C, Table 7). However, for semi-natural calcareous grassland a shift in species composition was recorded which was indicated either by a decline (e.g. of the dominant grass species *Festuca rubra* or *Campanula rotundifolia*) or an increase (*Galium verum* and *Plantago lanceolata*) in cover or frequency of species (Thwaites et al. 2006) and exhibited a general trend towards a more calcareous grassland community when treated with ozone (Ashmore et al. 1995). Bassin et al. (2007b) concluded, that in an old, multispecies community species-rich Geo-Montani-Nardetum pasture effects of elevated ozone on the productivity and floristic composition seem to develop slowly, as the vegetation responded without changes resulting from elevated ozone within three years of treatment. This low sensitivity was even confirmed when the experiment run for the longer term (seven years, Bassin et al. 2013). With respect to species-specific traits Bassin et al. (2009) suggested that commonly used principles of functional growth analysis do not directly hold under the specific conditions of such old, subalpine plant communities. As a second reason an adaptation to oxidative stress of the alpine species was discussed to account for the low sensitivity in response to the chronic low-level exposure used in this experiment (Bassin et al. 2013).

5.1.1.2 Artificial grassland communities

As a generally accepted outcome of screening experiments with single plants or monocultures (see chapter 3) it has been shown that members of Fabaceae (legumes) in general and the genus *Trifolium* in particular belongs to the most sensitive plant species, whereas members of the family Poaceae were significantly less responsive to ozone. Based on these findings, and because of their high frequency and relevance for the ecosystem function of managed and low-managed grasslands, experimental activities on effects of ozone on interspecific competition between herbaceous plant species mainly focused on grass clover mixtures, however, recently, there is an increasing number of studies on other species either as a two-species phytometer approach or by newly established model plant communities.

5.1.1.2.1 Growth effects on two-species communities

In the 1980s and 1990s, several experiments designed to study ozone effects on competition were carried out by sowing a grass / clover mixture in the field (see Annex C, Table 8), however, the majority of studies was done by using potted communities (see Annex C, Table 9). As been predicted from the knowledge about their relative sensitivity the main effect on artificial grass/clover mixtures could be attributed to a marked negative growth response of the clover, whereas the grass species was not impaired by ozone (Bennett & Runeckles 1977; Montes et al. 1982; Nussbaum et al. 1995; Haldemann & Fuhrer 2005; González-Fernández et al. 2008; Hayes et al. 2009; 2010a). If the total biomass of the mixture was largely influenced by the more sensitive component a decline in total yield of the mixture has been recorded: (*Trifolium repens* / *Lolium perenne,* Hayes et al. 2009; *Trifolium repens* / *Festuca arundinaceae,* Montes et al. 1982 or *Trifolium pratense* / *Trisetum flavescens*, Nussbaum et al. 2000). On the other hand, a wide range of experimental exposures to elevated ozone resulted in unchanged total yield quantities for perennial species (e.g. *Trifolium repens / Lolium perenne,* González-Fernández et al. 2008), or annual species (*Trifolium incarnatum* / *Lolium multiflorum*, Bennett 1976; or grass / alfalfa, Johnson et al. 1996) and is the expression of the fact that an ozone induced decline in the relative yield of clover entailed an increase in the relative yield of the grass component by enabling to populate resulting gaps which has been evidenced for different species mixtures (Bennett 1976; Nussbaum et al. 1995; Haldemann & Fuhrer 2005; González-Fernández et al. 2008; Hayes et al. 2009). Consequently, any change in the legume:grass ratio was dominated by the sensitive response of the legume component and positive effects on the grass component are a consequence of growing in mixture with a sensitive species.

Furthermore, this effect could be strengthened because altered root/shoot ratios (Haldemann & Fuhrer 2005) and reduced remobilization of reserves after grazing (Nussbaum et al. 2000) could favour less sensitive species. Thus, ozone may interact with cutting by reducing the capacity for regrowth from energy reserves (Ashmore & Ainsworth 1995). Johnson et al. (1996) demonstrated an ozone induced increase in shoot growth of the grass corresponding to a decrease in the legume species even if the below-ground competition was experimentally excluded. These findings from experiments with potted plants have also been verified in field experiments: In a *Trifolium repens* / *Festuca arundinaceae* field the more sensitive response of clover either dominated the total forage yield that was reduced (Blum et al. 1983) or the growth of the grass was stimulated indirectly (Rebbeck et al. 1988; Heagle et al. 1989). When grown in competition with *Lolium perenne,* Wilbourn et al. (1995) found a persistent effect of ozone on yield and stolon density of *Trifolium repens* associated with a significant loss of total yield.

In some studies the effect of ozone on the competition within a two-species mixture without legumes was investigated. Competitive ratios of *Andropogon gerardii* and *Sorghastrum nutans* were shown to be altered significantly by ozone (Endress & Iverson 1999), although the effects were rather small. Using a phytometer approach (*Agrostis capillaris* and *Poa pratensis*, respectively) the response of early season ozone stress on model communities of wet grassland species (Tonneijck et al. 2004) and low-managed grassland species (Bender et al. 2002; Bender et al. 2003; Bender et al. 2006) were investigated over three seasons. Although ozone levels exceeded the proposed critical level for the adverse effects of ozone on semi-natural vegetation, for none of the ten species impacts on growth were detected when grown in monoculture. Target species differed significantly in their competitive ability but they did not provide clear evidence that interspecific competition altered the harmful effects of early season ozone on above ground growth. However, for one species, *Veronica chamaedrys*, ozone was shown to affect its competitive ability against *Poa pratensis* negatively (Bender et al. 2002; Bender et al. 2003). More recently, a similar increase in the grass cover ratio was demonstrated for *Anthoxanthum odoratum* and *Dactylis glomerata*, respectively, when grown in competition with *Leontodon hispidus* (Hayes et al. 2011).

5.1.1.2.2 Growth effects on model plant communities

In a field-sown pasture composed of grasses, clover and weeds, the dominant effect of decline in both clover components, *T. repens* and *T. pratense*, was associated with a slight increase in the yield of grasses (Fuhrer 1994; Fuhrer et al. 1994). At three more sites the response on potted complex model plant communities consisting of up to seven species and up to ten individuals or even more have been investigated (see Annex C, Table 9).

In none of their related experiments of Ashmore & Ainsworth (1995) and Ashmore et al. (1996) the total biomass was reduced by increasing ozone exposure but effects were found on the biomass of individual species and the proportion of forbs in the total biomass: A decline of *Trifolium repens* with increasing ozone was associated with an increase in biomass of *Festuca rubra* in cut pots and *Agrostis capillaris* in uncut pots, respectively, emphasizing the importance of cutting or grazing. In a community representing typical upland grassland, *Anthoxanthum odoratum* was most affected in terms of above-ground biomass reduction and this effect contributed to a decrease in total community biomass and grass:forb ratio (Hayes et al. 2010b). In Finland, after only two years of moderate (40 ppb) exposure to ozone the total early season coverage of plant communities was decreased (Rämö et al. 2007), but changes in the dominance of different functional groups did not occur (Rämö et al. 2006).

5.1.1.3 Modification of the response to ozone by the presence of a competitor

Beside these effects on relative yield, however, there is some evidence that the presence of an interspecific competitor (grass) may affect the response of the clover species to ozone: In two-species mixtures, adverse effects of ozone on productivity may by enhanced (*Trifolium pratense* in comp. with *Trisetum flavescens*, Haldemann & Fuhrer 2005) or mitigated (*Trifolium incarnatum* in comp. with *Lolium multiflorum,* Bennett & Runeckles 1977 and *Trifolium repens* in comp. with *Lolium perenne,* González-Fernández et al. 2008). Hayes et al. (2010a) reported on a neighbour effect on the proportion of injured leaves, showing an increase in clover and decrease in the grass due to the presence of the interspecific competitor. Bender et al. (2006) indicated a significant influence of interspecific competition on the extent of the injuries on plants of *Poa pratensis,* which were most sensitive when grown alone, whilst the presence of a competing species reduced the extent of injured leaves. Similarly, in terms of senescence plants of *Holcus lanatus* and *Molinia caerulea* were shown to be more sensitive to ozone in monoculture compared to the mixed culture with *Agrostis capillaris* (Tonneijck et al. 2004), and *Leontodon hispidus* exhibited a larger increase in ozone-induced senescence observed in the more open canopy of *A. odoratum* compared to the denser canopy of *D. glomerata* (Hayes et al. 2011).

Based on these findings the question arose, whether the uptake of ozone can be modified by a neighbouring plant. Hayes et al (2011) gave evidence to support this theory as they measured a reduced stomatal conductance of inner canopy leaves of *L. hispidus* grown with *D. glomerata* compared to when grown with *A. odoratum.*

Hayes et al. (2010a) suggested that different mechanisms appeared to influence the interaction between response to ozone and competitors in these two species. Modification of the canopy structure and microclimate seem to be important parameters. *Trisetum flavescens* responded more strongly in mixture with a low stature species (*Centaurea jacea*) than in mixture with *Trifolium pratense* (Nussbaum et al. 2000). In contrast, it has been suggested that the sensitivity *Trifolium pratense* depend on the canopy structure as in mixture with the tall-stature grass species penetration of ozone was increased in the canopy being less dense than in monoculture (Haldemann & Fuhrer 2005).

Lin et al. (2007) reported on ozone-induced shifts in proportions of plant functional groups in a species-rich pasture which were associated with alterations in its nutritive quality. Similarly, in two-species model-communities, the effect of ozone on the quality of the grass component depended on the competing species (Blum et al. 1983; Bender et al. 2006). A decrease in the nutritive quality of *P. pratensis* due to ozone was greatest when competing with *Veronica chamaedrys.* while an increase in lignin concentration was greatest in competition with *Achillea millefolium* (Bender et al. 2006). In this experiment the role of *V. chamaedrys* and *A. millefolium* as competitors for the ozone susceptibility of *P. pratensis* was supported by means of the biochemical stress response: *P. pratensis* exhibited a different behaviour against ozone depending on the competing species, showing an overall higher sensitivity to ozone in mixture with *A. millefolium*. On the other hand, on *V. chamaedrys* the effects of ozone were amplified by the competition with the *P. pratensis* (Scebba et al. 2006)*,* thus affecting its competitive ability *(*see 5.1.1.2.1*)*.

Considering characteristic species of therophytic dehesa grasslands flower production of *Trifolium cherleri, Trifolium subterraneum* and *Trifolium striatum* was suppressed by ozone and by competition with *Briza maxima* but an effect of competition on the response to ozone was absent (Gimeno et al. 2003). Moreover, in complex model communities there is evidence of ozone impacts on flowering: For *Lotus corniculatus* timing and number of flowers was accelerated by ozone (Hayes et al. 2012). A significant reduction in flower numbers with increasing ozone was found for *Campanula rotundifolia*, *Scabiosa columbaria*, and *Vicia cracca* (Rämö et al. 2007; Hayes et al. 2012). Such changes in flowering timing and number could have severe ecological impacts with implications for pollination and the long-term outcome of the whole community as well as probable consequences on organisms in other trophic levels.

5.1.1.4 Summary

In summary, the studies clearly indicate that ozone may affect growth and vitality of natural grassland communities and show evidence of detrimental effects on species balance due to the exposure to ozone. This finding has been proved by both, the evaluation of the phytotoxicity of current ambient air by the use of ozone exclusion as reference (Heagle et al. 1989; Fuhrer et al. 1994; Ashmore et al. 1995; Pleijel et al. 1996) and the treatment with elevated levels of (Ashmore & Ainsworth 1995; Wilbourn et al. 1995; Ashmore et al. 1996; Rämö et al. 2006; Rämö et al. 2007; Hayes et al. 2010b).

In clover:grass mixtures a shift in species composition in terms of cover or abundance is the predominant effect, favouring the tillering of the grass component, whereas the effect on the total forage yield was determined by the susceptibility of the individual species. If exposure to high levels of ozone is going on Fuhrer (1997) concluded that the decline of white clover in managed grasslands will accelerate. Additionally, within two-species mixtures of non-legume plants the occurrence of ozone impacts on the competitive ability of constituent species has been evidenced by means of nutritive quality, biophysiological stress response, and onset of flowers. The findings demonstrate the complexity in response patterns of a semi-natural grassland community with respect to its species composition.

Although, any short-term disturbance in legume:grass ratio indicates the first disorder leading to a longer lasting establishing shift in species balance the understanding of its long-term effects in real communities is much more complicated. Research on old established communities implicate the difficulty, that the system examined is always the result of an adaptation to those ozone levels which for example were used as the reference levels (ambient air) in free air exposure systems.

The lower susceptibility of old, species rich grassland communities to ozone involves specific characteristics of themselves: Low productivity vegetation such as subalpine grassland is mainly composed of species with a stress-tolerant growth strategy, which have been considered unresponsive to ozone (Bassin et al. 2007a). The high genetic diversity and the large rooting system, which entails resources to allow repeated establishment of a new photosynthetic canopy are offering the system a large resilience against declining biomass production (Bassin et al. 2007a; Bassin et al. 2007b; Volk et al. 2011). In contrast, experiments with newly established grassland done by Rämö et al. (2006, 2007) indicate that nitrogen-poor meadows are potentially a very sensitive ecosystem. Also, mesotrophic grassland communities are characterized by the occurrence of faster growing species with are known to be more susceptible to ozone than the slower growing calcareous grassland species (Ashmore et al. 1995) and in fact, the experimental work of Wedlich et al. (2012) demonstrated the higher responsibility of such a community.

Several mechanisms are being discussed to explain the effects observed e.g. by Fuhrer (1997). Kochhar et al. (1980; 1982) referred to chemical interactions between species since leaf leachates of *F. arundinacea* influence the growth of *T. repens* in different ways, depending on whether the grass plants were ozone treated or not. A second important parameter is the characteristic of the canopy structure. Small-stature species growing in the lower portion of the canopy are better protected, because limited amounts of ozone diffuse through the canopy (Fuhrer 1997). Thus, a modification of the ozone response of a species by the presence of a competitor is thought to be related to a modification in its uptake of ozone. The measurements of Hayes et al. (2011) supported this idea.

5.1.2 Forests

Results of studies on ozone effects on competition between woody plants and interactions between woody and understory plants in established or artificial forest plant communities are shown in (see Annex C, Table 10).

5.1.2.1 Established communities

In the 1980s and 1990s single studies have been performed to investigate the effect of ozone and other air pollutants on sensitivity of understory species growing in an intact conifer forest (Nygaard 1994) or beech forest (Steubing et al. 1989). With regard to community composition, Barbo et al. examined the response to sub-ambient and enhanced ozone levels of an early successional plant community associated with *Pinus taeda*: Already within the first year the abundance of the five most common species was affected (Barbo et al. 1995). Barbo et al. (1998) concluded, that total vegetative cover, vertical density of foliage, and species richness, diversity and evenness have been influenced by current ozone exposures. However, contrary to the expectations based on previous studies, *Pinus taeda* showed an contrasting response to ozone, that mean reduced growth in CF, when grown in competition with understory vegetation (Barbo et al. 2002).

It is in the nature of the things that examination of forest ecosystems is incomparably complicated. While open top chamber approaches are suitable to investigate the response of young trees and understory, in case of mature stands more complex, more expensive and effortful facilities are required. In Germany, a group of beech and spruce trees within a 55-year-old Norway spruce stand has been exposed to experimentally enhanced free-air ozone fumigation using a novel methodological approach (Kranzberger Forst, Rust & Roloff 2009). Beginning in the year 2000, 20 research teams examined different issues including growth and competitiveness. Individuals of both tree species spruce and beech grew faster in mixture than in pure stands reflecting a facilitation of spruce and reduction in competitiveness of beech. New insights into the influenceability of competitiveness of mature trees by a stressor as ozone are limited or rather have to be deduced indirectly from findings concerning physiological issues or resource availability. The results of the 'Kranzberger Forst' interdisciplinary research project led to the conclusion that increasing levels of stress, will change the pattern of carbon allocation in mixed stands of beech and spruce and the outcome of competition (Pretzsch & Schutze 2009). Finally, Pretzsch et al. (2010) demonstrated a shift in the resource allocation in mature trees caused by exposure to high ozone. Accompanying studies at different ozone levels have been performed in exposure chambers and will be shown in chapter 5.1.2.2. Using simulations from the plant-growth model PLATHO, Schulte et al. (2013) analysed mechanisms of competition and found that other parameters than ozone (and CO_2) alter the positive asymmetric competition for light and the symmetric competition for water among beech and spruce individuals grown in monoculture.

5.1.2.2 Artificial forest communities

The artificial tree communities mentioned here, always consist of young seedlings or saplings, experiments on older stands will be shown in chapter 5.1.2.3. There are only two investigations we were able to find in which the response to ozone of a tree species was studies in competition with either a grass species or second tree species. On *Pinus ponderosa*, after three years of ozone exposure in open top chambers, significant growth reductions only occurred when growing in competition with the grass *Elymus glaucus* (Weber et al. 1997; Andersen et al. 2001). The authors suggested that in the presence of competition ozone-exposed ponderosa pine seedlings appeared to be unable to obtain sufficient nitrogen because compensation mechanisms were not sufficient when both treatments were combined.

Under standardized phytotron conditions, parameters related to the competition between *Fagus sylvatica* and *Picea abies* have been analysed. The results clearly indicated that the responses to ozone strongly depend on the type of competition: *P. abies* showed a competitive advantage relative *to F. sylvatica*, which in turn was more susceptible to ozone. Although the response to ozone of *P. abies* was not significantly affected by either intra- or interspecific competition, the competitive ability of this species was slightly affected by exposure to ozone as indicated by an enhanced aboveground growth of the competing *F. sylvatica* plants (Grams et al. 2002; Liu et al. 2004; Kozovits et al. 2005a). Under conditions of interspecific competition, *P. abies* was found show superiority in nitrogen (N)- acquisition whereas *F. sylvatica* in turn appeared to be N-limited (Kozovits et al. 2005a; Grams & Matyssek 2010). Effects on nutrient efficiency indicate that processes of stress defence due to ozone exposure trigger a nutrient demand at the expense of above-ground competition (Rodenkirchen et al. 2009). In general, the capability of *F. slvatica* to sequester and retain nutrients was lower in mixed than in monoculture (Kozovits et al. 2005b). Furthermore, ozone stress reduced ^{15}N uptake and nutrient efficiencies (N and P, Rodenkirchen et al. 2009; Grams & Matyssek 2010), and gas exchange and photosynthetic discrimination against $^{13}CO_2$ (Grams & Matyssek 2010). A reduction of carbohydrates, however, became only apparent in monocultures (Liu et al. 2004).

5.1.2.3 Aspen-FACE

The Aspen FACE (Free-Air Carbon dioxide Enrichment) facility near Rhinelander, Wisconsin, USA, is the world's largest open-air climate change research facility, and the only FACE site where woody plants are being fumigated with elevated CO_2 and ozone, singly and in combination. Stands of *Populus tremuloides* (aspen) have been established in 1997, consisting of different aspen clones or mixed stands with either *Betula papyrifera* or *Acer saccharum*.

Clear differences have been determined between clones of *P. tremuloides* as the magnitude of ozone effects on growth depended on clone and competitive status (McDonald et al. 2002; Kubiske et al. 2007) and N acquisition (Zak et al. 2007b). One clone, for example, responded to ozone in monoculture but not when competing with *A. saccharum.* In total, after seven years of exposure ozone slightly increased the conversion of a *P. tremuloides* stand to a *B. pendula* stand (Kubiske et al. 2007), whereas the cumulative N acquisition was decreased in both species (Zak et al. 2007b). When the experiment went on for 12 years, Zak et al. (2012) found, that the rank order of N acquisition among *P. tremuloides* genotypes was not changed over time, i.e. when juvenile trees mature. Soil N and ^{15}N acquisition by the *P. tremuloides* genotype common in each mixed communities was not affected by ozone, regardless of competitive interactions (Zak et al. 2012).

The understory community consisted of more than 30 species and was dominated by perennial oldfield vegetation. Effects on total and individual species biomass, N content, and ^{15}N recovery could not be related directly to different ozone treatments but reflect the effects on the structure of overstory community, which is determined by the tree species present and their response to the treatments (Bandeff et al. 2006). In a multiple-year survey, even the abundance of clover species, which are known to be most sensitive, exhibited no response (Awmack et al. 2007). It was concluded, that sensitive genotypes might already be eliminated during the previous development of the community.

In summary, the results clearly indicate that high levels of ozone have the potential to alter the strength of intraspecific competition within aspen populations and the interspecific competition between tree species (aspen and birch). As a consequence, understory vegetation was greatest under the more open canopy of the elevated ozone treatments.

5.1.3 Agro-ecosystems: weed crop interaction

As already mentioned for grassland, any differential susceptibility of two plant species in terms of growth or fitness may alter competitive interactions, and this is also assumed for crop-weed interactions. Unfortunately, knowledge about this issue is rather low.

The group of Grantz assessed ozone impacts on competition between crops and yellow nutsedge (*Cyperus esculentus*), a C-4 weed, which was shown to allocate greater resources to reproductive structures (tubers) under elevated ozone (Shrestha & Grantz 2005; Grantz & Shrestha 2006). However, more recent studies revealed a reduction of belowground sink strength due to moderately enhanced ozone levels (Grantz et al. 2010). In competition with *Lycopersicon esculentum* the weed reduced tomato productivity under low and moderate ozone concentrations, whereas the crop in the absence of the weed responded only to high ozone levels (Shrestha & Grantz 2005). Growing together with *Gossypium barbadense* ozone impacts were exacerbated by *C. esculentus* (Grantz & Shrestha 2005) suggesting that rising ozone concentrations appear likely to increase the competitiveness of nutsedge with respect to cotton (Grantz & Shrestha 2006). More recently, Grantz et al. (2010) predicted that ozone will increase the competitiveness of nutsedge with respect to specific crops, thus increasing the level of threat to agricultural production from *C. esculentus*.

In the 1980s Cornelius & Markan (1984) reported on modified interference between the two weed species *Chenopodium album* and *Urtica urens* due to ozone as a slight competitive advantage of *C. album* was enhanced. Pfleeger et al. (2010) studied the response of a plant community emerging from a farm soil over several generations. Individuals from some of the species appeared to be diminishing in number by the third year such as *Capsella bursa-pastoris, Erodium cicurtarium,* and *Spergula arvensis*. However, changes in competitive interactions and community dynamics seemed to be rather an indirect effect of premature senescence of taller species via altered light availability.

5.1.4 Conclusion

In the majority of long term fumigation experiments exposure to elevated ozone had only marginal effects on the total productivity of a plant community, especially pronounced for grassland communities. The response being predominant was a decline in the most sensitive species associated with an increase in the more tolerant one, thus the resulting answer of the total community was determined by the sensitivity of its components. In artificial forest communities, the presence of a (weed) competitor was shown to reduce the nutrient uptake and efficiency. For both, there is increasing evidence that ozone may actually affect the competitive balance of a two-species model system.

On the other hand, it has been evidenced that the response to ozone of a species may be modified by introducing interspecific competition. Although the underlying mechanisms remain still unclear, the role of root leachates and the alteration of the canopy structure being related to an alteration of ozone uptake have been discussed. Therefore, to better understand how elevated ozone will shape the composition and genetic structure of a plant community, more emphasize should be put on belowground competition and the application of a multi-layer approach to modelling uptake of ozone sensu Jäggi et al. (2006), and to include the use of process-level models (Andersen & Grulke 2001).

The results clearly indicate that to establish critical levels for ozone to protect vegetation from harmful effects the consideration of individuals' and species' interactions in complex systems within longer lasting experiments on (established) communities is needed. Andersen & Grulke (2001) further proposed that additionally to the continuing research into the mechanisms of response to ozone, "a better understanding of how ecosystems already exposed to stress function in the presence of ozone is required".

5.2 Plant-pathogen interaction

Among the interactions of ozone with biotic factors plant pathogens and insect pests have repeatedly been studied in various experimental approaches (Percy et al. 2003; Eastburn et al. 2011). For crops knowledge on plant-pathogen interactions have been summarised by Manning & von Tiedemann (1995) and Krupa et al. (2001). They concluded that effects on pathogens are plant-mediated and are unlikely to base directly on adverse effects of the pollutant.

5.2.1 Exposure experiments

For **crops** growth and yield reduction may generally be induced by both, pathogen infection and exposure to elevated ozone as shown, for example, for wheat *Triticum aestivum* (Pearce 1996; von Tiedemann & Firsching 1998; 2000), and both factors may interact in various ways. On the one hand, disease severity was found to be enhanced significantly by raised ozone concentrations e.g. for powdery mildew (*Erysiphe graminis f.sp. tritici, Septoria nodorum,* and *Bipolaris sorokiniana*, von Tiedemann et al. 1991; von Tiedemann & Pfaehler 1994). These studies carried out in climate chambers or OTCs indicated that ozone-induced senescing effects and leakage of nutrients from leaves may be regarded as the main factors in predisposing wheat for necrotrophic leaf pathogens. Moreover, it was observed that ozone effects on the susceptibility of the pathogen depended on growth stage of the host plant (*S. nodorum,* von Tiedemann & Pfaehler 1994) or the pathogen susceptibility of the genotype, whereas ozone sensitivity significantly correlated with disease development of tan spot fungus (*Pyrenophora tritici-repentis,* Sah et al. 1993).

On the other hand, leaf rust (*Puccinia recondita f. sp. tritici*) disease on wheat did not interact with elevated ozone (Pfleeger et al. 1999) or was inhibited by ozone exposure, while ozone injury was more severe on rust infected plants (von Tiedemann & Firsching 1998; 2000). On *Hordeum vulgare*, resistance against *Drechslera teres* increased after exposure to twice ambient concentrations of ozone in climate chambers associated with higher levels of beta-1,3-glucanase and chitinase in barley leaves (Plessl et al. 2005). Manning & von Tiedemann (1995) summarised that increased susceptibility after ozone exposure can be expected for necrotrophic pathogens while obligate biotrophic infections tend to be diminished by ozone.

The fact that different pathogen types interact differently with ozone has also been shown for other host-pathogen interactions: Ozone treated plants became either more susceptible to the pathogen, e.g. *Phaseolus vulgaris* towards *Sclerotinia sclerotiorum* and *Botrytis cinerea* (Tonneijck & Leone 1993) and *Solanum tuberosum* towards late blight pathogen *Phytophthora infestans* (Plessl et al. 2007) or more resistant e.g. *Pisum sativum* towards powdery mildew *Erysiphe polygoni f. sp. pisi* (Rusch & Laurence 1993), a behaviour which also was apparent towards a viral infection with soybean mosaic virus (SMV, Bilgin et al. 2008). An induction of basal defines mechanisms by ozone including fungal, bacterial, and viral defines-related genes was evidenced for *Glycine max* (Bilgin et al. 2008). The authors assumed that this way, atmospheric ozone may alter the co-evolutionary relationship of plant-pathogen interactions in the future.

For coniferous **trees** an increased susceptibility caused by ozone was found for the root and butt rot pathogen *Heterobasidion annosum* on *Picea sitchensis* (Pearce 1996) and the pitch canker fungus *Fusarium subglutinans* on *Pinus taeda* (Carey & Kelley 1994) causing a synergistic response to both, the abiotic and the biotic stressor. When grown in mixture with *Fagus sylvatica* susceptibility to the root pathogen *Phytophthora citricola* of *Picea abies* was increased, while ozone apparently raised the defence capacity in beech. Belowground competitiveness was thought to be responsible for this species-specific response and was described as follows: Ozone limited growth, photosynthesis, and N uptake of beech and provided resistance against the pathogen while spruce profited from the lower resource acquisition of beech, as a result, spruce displayed enhanced susceptibility and no biochemical impact (Luedemann et al. 2005; Luedemann et al. 2009). For *F. sylvatica* alone inoculation with *P. citricola* after three years of 4-yr fumigation period did not affect plant growth, and predisposing to ozone did not influence the root infection (Fleischmann et al. 2009; Winkler et al. 2009). Exposure to ozone of adult trees inoculated with endophytic *Apiognomonia errabunda* initially exhibited a marginally inhibitory effect on fungal colonization but this protective effect disappeared in the course of the vegetation period. Nevertheless, climatic factors such as heat periods are thought being more pronounced than ozone treatment (Bahnweg et al. 2005; Olbrich et al. 2010).

Further experiments related to the interaction with pathogens and a deciduous tree species have been performed by using *Populus* spec. plants. Exposure to moderate levels of ozone was shown to increase the incidence of leaf spot and canker disease *Mycosphaerella populorum* (Woodbury et al. 1994) and *Marssonina tremulae* (Beare et al. 1999b), while acute exposures to 200 ppb ozone inhibited the spore germination of *M. tremulae*. Severity of aspen rust infection (*Melampsora spec. or M. medusae*) was found to be increased by ozone both in closed chambers (Beare et al. 1999a) and due to natural infection under free-air exposure (Karnosky et al. 2002; Percy et al. 2003). The predisposing effect has been explained with the ability of ozone to alter leaf surface properties such epicuticular waxes (Karnosky et al. 2002; Percy et al. 2003).

There was only one study we became aware of which applied to the interaction of pathogens and grassland plant species and has been published years ago. Kochhar et al. (1982) exposed *Trifolium repens* and *Festuca arundinacea* plants inoculated with the soil-borne pathogen *Rhizoctonia solani* singly and in mixture to ozone. Initially, ozone and the pathogen both reduced biomass of clover synergistically, but in the presence of multiple ozone exposures the stress from *R. solani* was lost. Effects on fescue were less pronounced than on clover.

5.2.2 Implication for field surveys

In the Californian San Bernardino Mountains long-lasting exposure to high levels of ozone had various detrimental effects on plant growth and health which were most pronounced for pine trees (see chapter 7). When estimating the relevance of the contributing factors, frequently an interaction with the fungus *Fomes annosus* (syn. *Heterobasidion annosum*) was assumed to amplify oxidative stress. For experimentally inoculated *Pinus ponderosa* and *P. jeffreyi* the severity of infection with *F. annosus* significantly correlated with the leaf surface injured by oxidants i.e. mainly ozone, at least at one site in California (James et al. 1980b; James et al. 1980a). Similarly, black stain root disease, caused by *Leptographium wageneri var. ponderosum* increased as the ozone exposure within OTCs increased on *P. ponderosa* (Fenn et al. 1990). Therefore, especially for pines it was assumed that weakened trees may become more susceptible to root pathogens (Miller 1985; Krupa & Manning 1988) and for further risk assessments estimating the impact of ozone on the susceptibility to root pathogens such as *F. annosus* and *L. wageneri* was recommended. However, occurrence of ozone symptoms on *Pinus strobus* grown in plantations in North Carolina, USA, could not be related to the incidence of root diseases by *F. annosus* (Leininger et al. 1990). More recently, on *Picea sitchensis* the resistance to *F. annosus* was reduced due to an exposure to 120 ppb in a CF-greenhouse (Pearce 1996) but remained unchanged due to moderately enhanced ozone levels in free-air (AA/1.3xAA (Pearce & McLeod 1995). However, under both experimental conditions the levels of main constitutive antifungal compounds in spruce did not change. In established ecosystems, a plant-pathogen system considered may interfere with other biotic factors which potentially superimpose the effect studied. For example, mycorrhizal infection with *Hegeloma crustuliniforme* protected *Pinus sylvestris* from ozone-induced increase in disease incidence by *F. annosus* (Bonello et al. 1993b). Another explanation for the various observations may be found in weather condition. Although ozone-induced metabolic changes can persist in plants over days or months (Sandermann 2000). Boland et al. (2004) submitted that periods of high ozone concentration did not coincide with environmental conditions suitable for infection by most fungal pathogens.

5.3 Plant-herbivore interaction

Exposure to ozone may alter chemical composition and, in this way, nutritional quality of foliage as well as the defence capacity by secondary chemistry (Valkama et al. 2007; Bidart-Bouzat & Imeh-Nathaniel 2008), see also chapter 6.4). As a result of this, it has frequently been observed that performance, reproduction behaviour, or development of herbivore insects was affected by exposure of host plants to ozone. Holopainen (2002) reviewed the response of aphids to elevated CO_2 and discussed its interaction with air pollutants and reported on both, decreased or increased aphid growth on the same plant, depending on duration and level of exposure. Valkama et al. (2007) concluded from their meta-analysis reviewing 63 studies conducted on 22 species of trees that elevated ozone had positive effects on insect performance as pupal mass increased and larval development time shortened.

Studies using artificial diet techniques showed that the direct effect of ozone on herbivores was thought to be unimportant (Brown et al. 1992; Jackson 1995). However, the hornworm moth *Manduca sexta* preferred ozone-exposed tobacco plants to oviposit eggs but these preferences were existent only if ozone is present in the atmosphere (Jackson et al. 1999; Jackson et al. 2000). Thus, it is widely believed that impact on performance of herbivores is a result of an interference with their feeding preferences.

5.3.1 Alteration of feeding preferences

Early studies provided evidence that herbivores prefer foliage from plants which have been exposed to elevated ozone e.g. gypsy moth (*Lymantria dispar*) on *Quercus alba* (Jeffords & Endress 1984) or Mexican bean beetle (*Epilachna varivestis*) on *Glycine max* (Endress & Post 1985).

On some crops a synergistical interaction of both the biotic and the abiotic stressor was indicated by an improvement of the performance of parasites by ozone. This was shown for nematodes on *Lycopersicon esculentum* (Khan & Khan 1998), Russian wheat aphid (*Diuraphis noxia*) on *Triticum aestivum* (Summers et al. 1994), hornworm moths (*Manduca sexta*) on *Nicotiana tabacum* (Jackson et al. 1999; Jackson et al. 2000), or tomato pinworms (*Keiferia lycopersicella*) on *L. esculentum* (Trumble et al. 1987). On the other hand no interactive effects have been reported for rose grain aphid (*Metopolophium dirhodum*) on cereals (Jackson 1995), Colorado potato beetle *Leptinotarsa decemlineata* on potato *Solanum tuberosum* (Costa et al. 2001), aphids (*Aphis glycines*) and Japanese beetles (*Popillia japonica*), respectively on *Glycine max* (Dermody et al. 2008; O'Neill et al. 2008). Nonetheless, several recent exposure experiments revealed a negative effect on the performance of parasites under elevated ozone (whitefly *Bemisia tabaci* on *L. esculentum*, Cui et al. 201) and maize stalk borer *Chilo partellus* on *Zea mays,* Mina et al. 2012b; Mina et al. 2012a).

Results of Brown et al. (1992) obtained with *Aphis fabae* on *Vicia faba* indicated that the response may depend on exposure duration as within the first 24 h of exposure to ozone (100 ppb) induced an increase in mean relative growth rate (MRGR) of aphids and a prolonged exposure resulted in a decreased growth.

By taking the example of one long-term experimental set-up, the Aspen FACE study, it shall be demonstrated how variable the host-herbivore-atmosphere interaction might be. On *P. tremuloides* elevated ozone decreased leaf beetle *Chrysomela crotchi* performance (Vigue & Lindroth 2010), reduced colonization rates and increased male development time of the aspen blotch leafminer *Phyllonorycter tremuloidiella* (Kopper & Lindroth 2003a), but improved the performance of forest tent caterpillar (*Malacosoma disstria*) larvae (Holton & Lindroth 2001; Kopper & Lindroth 2003b),and had no effect on invasive weevil *Polydrusus sericeus* (Hillstrom et al. 2010).

Frequently the performance of aphids on conifers has been investigated. On *Picea sitchensis* the aphid *Cinara pilicornis* was affected by ozone, whereas *Elatobium abietinum* did not response (Brown et al. 1993). On ozone-exposed seedlings of *Pinus sylvestris* the MRGR of lygus bug (*Lygus rugulipennis*) nymphs was lower than on seedlings exposed to ambient ozone, but sawfly (*Gilpinia pallida*) larvae grew better on elevated ozone seedlings whereas MRGR of aphids (*Schizolachnus pineti* and *Cinara pinea*) were not affected by ozone exposure (Manninen et al. 2000).These results clearly indicate a species-specific response as for the same host species exposure to ozone influenced herbivore species differentially. Moreover, it has been shown that the effect on aphids (*Cinara pilicornis* on *Picea abies*) may also depend on the developmental stage or age of the host, respectively, as elevated ozone during early shoot elongation period stimulated the population development of *C. pilicornis*, but on maturing shoots negatively affected the aphid performance (Holopainen & Kossi 1998).

5.3.1.1 Foliar biochemical composition

On *Pinus sylvestris* ozone concentrations up to 150 ppb did not significantly affect aphid performance (Holopainen et al. 1992) and growth rate (Brown et al. 1993) or the numbers of nymphs produced by grey pine aphid *Schizolachnus pineti* (Kainulainen et al. 1994), but significantly affected MRGR of the aphid and the total number of reproduced nymphs in a second experiment using similar conditions (Kainulainen et al. 2000). However, despite the difference in the outcome of the experiments the absence of an effect on aphids coincide with the absence of an effect on foliar biochemical composition, whereas the effect measured was associated with a simultaneously decrease in concentrations of monoterpenes and increased concentrations of free amino acids. Similarly, Holopainen et al. (1997) described the aphid performance on *P. sylvestris* and *P. abies* seedlings to be extremely variable and that occasions which led to an effect on aphids are suggested to represent episodes of high ozone concentration, which may increase free amino acids in foliage.

5.3.1.2 Dependence on host and host's susceptibility

A relationship to foliar biochemical composition became apparent on other species, too. Ambient ozone was shown to affect the aphid species *Aphis fabae* on *Phaseolus vulgaris* and *Phyllaphis fagi* on *Fagus sylvatica* differently compared to clean air (CF) and the response was related to ozone effects on the amino acid/sugar ratio within the phloem (Braun & Fluckiger 1989). Similarly, ozone significantly affected aspen (*Populus tremuloides*) foliar quality, whereas birch (*Betula papyrifera*) foliar quality was only marginally influenced (Couture et al. 2012). This difference seemed to be reflected by an ozone-induced increase in larval preferences of the forest tent caterpillar (*Malacosoma disstria*) for birch compared with aspen (Agrell et al. 2005), whereas a decrease in its performance was more pronounced on aspen (Couture et al. 2012).

These findings support the idea that ozone may influence the herbivore performance through altered foliar quality, thus, leading to the assumption that response of herbivore was mediated through the host plants and in particular their susceptibility to ozone. There is some evidence supporting this assumption: Growth of gypsy moth (*Lymantria dispar*) was affected negatively when feeding foliage from ozone treated seedlings of *Quercus alba* but not *Q. rubra* (Cannon 1993). Effects on the performance (developmental period and growth) of spider mites (*Tetranychus urticae*) depended on the ozone susceptibility of host plant (*Arachis hypogeae*, *Trifolium repens* NC-S and NC-R, Heagle et al. 1994; Hummel et al. 1998). Elevated ozone decreased leaf beetle *Chrysomela crotchi* performance on *P. tremuloides* especially if rearing on an ozone-sensitive genotype (Vigue & Lindroth 2010). By contrast, egg production and survival of Colorado potato beetle larvae (*Leptinotarsa decemlineata*) on *Solanum tuberosum* cultivars differing in their ozone susceptibility remained unaffected by ozone, irrespective from the severity of the impact on host (Costa et al. 2001).

5.3.2 Tritrophic systems

Beside this mutual dependency between host species or genotype and parasite species or genotype and its modification by ozone inclusion of their natural enemies represent a more complex level of investigation. For such a tritrophic system consisting of genotypes of *Populus tremuloides*, forest tent caterpillar *Malacosoma disstria*, and its dipteran parasitoid *Compsilura concinnata* it has been shown that elevated ozone could improve forest tent caterpillar performance and decrease parasitoid larval survivorship, depending upon the genotype (Holton et al. 2003). On paper birch (*B. papyrifera*) performance of aphids (*Cepegillettea betulaefoliae*) remained unaffected by ozone in the presence of natural enemy communities, whereas aphid populations increased significantly at elevated ozone when protected from natural enemies (Awmack et al. 2004). These studies were able to demonstrate that host-parasitoid interactions in forest systems may be altered by ozone.

Insects are known to communicate with each other through pheromones, which are likely to be destroyed by ozone losing their specifity (Arndt 1995; Klumpp et al. 1999) and this way may disturb the attraction of parasitoids and predators.

5.3.3 Effects on herbivore communities

As shown for wing induction on pea aphids (*Acyrthosiphon pisum*) on *Vicia faba* Mondor et al. (2005) suggested that environmental change such as CO_2 and ozone may alter also genotypic and phenotypic frequencies of herbivore populations, which consequently may result in altered community and ecosystem functioning.

In the aspen-birch stand (Aspen FACE) early summer censuses of phytophagous insect communities indicated that ozone and CO_2 affected insect biodiversity, depending on the tree species as species diversity was highest in elevated ozone treatment (Ashburn & Lindroth 2001). Elevated ozone reduced total arthropod abundance by 17 % and had a strong negative effect on parasitoid but also a positive influence on some sucking herbivores (Hillstrom & Lindroth 2008). This finding seems to correspond with the differential response on *P. tremuloides* depending on parasite as shown above. However, little is known, about the mechanisms of how ozone affects insect biodiversity.

An early report on a causal relation between severe parasite infestation and oxidant air pollutants can be found in 1968 (Cobb et al. 1968; Stark et al. 1968). In the forest stands in the Californian San Bernardino Mts. (see chapter 7) ponderosa pines (*Pinus ponderosa*) had been found to be killed by bark beetles (*Dendroctonus brevicomis* and *D. ponderosae*). Because beetles preferred trees injured by oxidant pollutants the air pollution was assumed to predispose *P. ponderosa* to bark-beetle infestation. This way, 36 trees in a 150-tree plot were killed over a 3-year period and in those days it was predicted that ponderosa pine will be virtually eliminated from the forest stands in this area if air pollution would continue unabated (Cobb & Stark 1970). Later on, Miller (1985) estimated mortality rates to amount to 4-6 % between 1973 and 1978. In terms of the population dynamics Dahlsten et al. (1997) presumed that the effect of a given population of western pine beetle on tree mortality depends on the proportion of oxidant damaged trees within a stand. Even in in the early 2000s, when ozone levels were known to be significantly reduced, tree mortality and beetle activity was obviously higher for trees at the high pollution site compared to the low pollution (Eatough Jones et al. 2004). Moreover, diversity or richness of herbivores in the San Bernardino Mts. showed patterns of change that followed the air pollution (ozone) gradient with oak herbivore communities showing the strongest effect (Eatough Jones & Paine 2006). Similarly, in the southern Appalachians variable mortality patterns of Fraser fir (*Abies fraseri*) may be caused by locally distributed air pollutants acting in combination with other types of stress including those caused by the balsam woolly adelgid (*Adelges piceae,* Hain 1987). In Europe, the abundance and dynamics of bark beetle *Ips typographus* populations was evaluated in 60-80 year old Norway spruce stands within the Carpathian Mts. In several cases, higher bark beetle populations were shown to be associated with the ozone level of the site (Grodzki et al. 2004).

5.3.4 Conclusion

Frequently, feeding preference of herbivore insects was shown to be affected by elevated ozone along with altered foliar biochemistry. Depending on *i.)* parasite species, *ii.)* its mode of life, *iii.)* the host species / genotype, and *iv)* the exposure level or dynamics the performance of herbivores may either be improved or decreased. For aphids, it is hypothesize that stress frequency, intensity, duration and timing, will affect the direction of response to exposure of plants to ozone and that there is no general air pollution-induced plant stress that triggers aphid outbreaks on plants (Holopainen 2002; Menendez et al. 2009).

Although, the impact of elevated ozone on biotic interactions is highly variable, there is evidence that the biodiversity of forest insect communities is likely to change under atmospheric conditions predicted for the future with further consequences for nutrient cycling in ecosystems.

5.4 Below-ground effects

Biotic soil processes comprise activity of soil organisms and their interactions with plants. Elevated levels of ozone may indirectly alter soil processes and organisms mediated by plants and their responsiveness to ozone. Hence, first indicators of below-ground influences on the biodiversity of an ecosystem are changes in root growth, root and soil respiration, litter decomposition, soil microbial biomass and in particular symbiotic associations, which finally might impact microbial or mesofauna community structure.

5.4.1 Root growth and soil respiration

A decrease in root biomass due to restricted carbon allocation has been detected for ozone exposed young *Populus tremuloides clones* (Coleman et al. 1996) and *Quercus rubra* seedlings (Kelting et al. 1995), whereas seedlings of *Pinus ponderosa* showed no effect (Tingey et al. 2006). In mature *Fagus sylvatica* elevated ozone altered the timing of fine root turnover but not the turnover rate itself (Mainiero et al. 2009). In contrast, a stimulation of fine-root production by elevated ozone has been shown for a *Populus tremuloides* community (Pregitzer et al. 2008) and adult *Fagus sylvatica* trees (Nikolova et al. 2010).

To put emphasis on meadows and pastures sensitivity screenings or competitive studies of grassland species revealed ozone induced reductions in root growth for single species such as *Lotus corniculatus* and *Anthyllis vulneraria*, (calcareous grassland, Warwick & Taylor 1995), *Achillea ptarmica*, *Cirsium dissectum*, *Lythrum salicaria* and *Molinia caerulea* (fen-meadows, Franzaring et al. 2000)), and *Medicago sativa* (Johnson et al. 1996; Renaud et al. 1997), or total community root biomass of meadow mesocosms (Manninen et al. 2005; Kanerva et al. 2008).

Decreased respiration rates of roots in response to elevated ozone have been measured for seedlings of *Pinus taeda* decreased (Edwards 1991) and cuttings of *Populus tremuloides* (Coleman *et al.*, 1996). However, there were no effects on *P. tremuloides* when growing in established communities of the Aspen-FACE (Larson et al. 2002) or at lower levels of ozone (King et al. 2001). Enhanced rates of soil respiration caused by ozone have been measured in an adult European beech/Norway spruce forest (Nikolova et al. 2010), on *Betula pendula* (Kasurinen et al. 2004) and *Pinus ponderosa* seedlings (Andersen & Scagel 1997) and are hypothesized to result from increased root exudation (Andersen 2000). On the other hand in bulk soil collected from a cropland (Bonello et al. 1993a) and in field experiments with *Populus tremuloides* (Pregitzer et al. 2006) soil respiration rates were reduced under elevated ozone. Similarly, the net ecosystem dark respiration of meadow mesocosms was decreased by ozone (Kanerva et al. 2007).

In conclusion, there is evidence that ozone may affect soil respiration rates but this effect highly depends on age or exposure conditions.

5.4.2 Litter decomposition

A second way by which conditions for soil organisms may by changed are alterations in quality or quantity of litter produced from ozone impacted plants. Kasurinen et al. (2007a) reviewed existing information about ozone effects on leaf litter and concluded that ozone effects on leaf litter chemistry were more obvious at high ozone concentrations. For instance, effects of ozone on litter quality have been reported for *Betula pendula* (Parsons et al. 2004; Kasurinen et al. 2006; Kasurinen et al. 2007b; Parsons et al. 2008) and *Rubus cuneifolus* (Kim et al. 1998). Furthermore, it has been shown that litter decomposition depends on the initial concentrations of lignin *R. cuneifolus* (Kim et al. 1998) or condensed tannins and phenolics *Populus tremuloides* (Liu et al. 2009). In consequence, decomposition of litter from ozone treated plants was retarded (Kim et al. 1998; Baldantoni et al. 2013). In experiments with 4-year-old *Fagus sylvatica* seedlings ozone did not affect the litter degradation (Schloter et al. 2005).

Ozone-induced changes in litter quality of *P. tremuloides* and *Betula papyrifera* communities lead to reduced inputs of hemicellulose and lignin (Liu et al. 2005; Meehan et al. 2010) and to a decrease in nutrient flux into the soil (Liu et al. 2007; Zak et al. 2007a). In contrast, Stoelken et al. (2010) reported on additional N incorporation into the soil down to 30 cm depth under *Fagus sylvatica*.

5.4.3 Soil microbial communities

Soil microorganisms are limited by the amount and type of plant-derived substrates entering soil and plant growth processes and rhizosphere microbial activity are interfering in a highly complex way. Thus, any slight disturbance in plant biochemistry that cause a change in composition and quantity of exudates or litter might be amplified by entailing changes in microbial biomass and / or community structure and function. For both, the organisms associated with the rhizosphere or litter it hast been postulated that ozone effects would elicit physiological changes in soil microbial communities.

Kasurinen et al. (2007a) reviewed existing information about ozone effects on leaf litter. Recent long-term studies indicate that there are some ozone effects on microbial functioning in the soil, although the onset of these microbial responses may take years. Aneja et al. (2007) characterized the phylogenetic diversity of microbial communities colonizing control and ozone-exposed litter from *Fagus sylvatica* and *Picea abies* and provided evidence that changed litter quality due to elevated ozone did influence the structure of litter-colonizing microbial communities. For example, a shift in the microbial community structure in response to ozone has been shown on 4-year-old *F. sylvatica* (Pritsch et al. 2009), moreover, its function in terms of the potential nutrient turnover has been lowered by elevated ozone (Schloter et al. 2005). In contrast, Esperschutz et al. (2009) observed higher rhizosphere microbial biomass and abundance of plant C utilizing microbes when *F. sylvatica* was treated with ozone. The fact that bulk soil functionality did not respond to ozone indicated that ozone influenced the community structure indirectly via changes in root exudation and rhizodeposition.

Investigating container-grown *Pinus ponderosa* Scagel & Andersen (1997) and Olszyk et al. (2001) supposed that elevated ozone tended to increase the ratio of active-fungal to active-bacterial biomass with increasing plant exposure to ozone. Later on, Tingey et al. (2006) showed that there were no effects on the abundance of culturable bacteria and fungi. Within the communities of the Aspen-FACE (*P. tremuloides, B. papyrifera*, and *A. saccharum*) elevated ozone significantly altered fungal community composition (Chung et al. 2006) as evidenced by phospholipid fatty acid analysis. Recently it was shown by means of qPCR analysis of fungal or bacterial rRNA genes of bulk soil (0-5 cm) collected from the aspen stand that fungal or bacterial biomass did not respond to eleven years of exposure to elevated ozone although the relative abundance of Basidiomycota fungi increased relative to Ascomycota (Dunbar et al. 2014).

Soil microbial communities also have been investigated within native herbaceous species or communities. For blue wildrye *Elymus glaucus* as a response to ozone a reduction in soil bacterial biomass and an increase in total fungi was described (Yoshida et al. 2001). Mesocosms that simulated hay meadows (constituted of *Agrostis capillaris, Anthoxanthum odoratum, Fragaria vesca, Campanula rotundifolia, Ranunculus acris, Trifolium medium,* and *Vicia cracca*) were exposed to elevated ozone over three years. Due to ozone bacterial, actinobacterial, and fungal PLFA (Phospholipid-derived fatty acids) biomass was shown to decrease (Kanerva et al. 2008).

A similar experiment succeeded in detecting a decrease in total actinobacterial biomass (PLEA - method) for *Lathyrus pratensis* but not for *Agrostis capillaris* (Manninen et al. 2010). The authors concluded that changes are considered to arise mainly from differences between the plant functional types (i.e. grass cf. N_2-fixing legume), in litter quality, and soil C:N ratio. In peatland microcosms (*Eriophorum vaginatum*) Morsky et al. (2008) found an ozone induced increase in microbial biomass at the end of a three-year lasting experiment due to ozone.

Dohrmann & Tebbe (2005) studied the rhizosphere bacterial community composition of five low managed grassland species grown in monoculture using genetic profiling of PCR amplified 16S rRNA gene sequences. They found that a five week exposure to elevated ozone did not select for a different bacterial community composition as neither bacteria-specific profiles nor those with a more narrow phylogenetic range picked up an ozone-triggered difference. Because these species did not express any symptoms of ozone injury above-ground (Bender et al. 2002) they extended their study to four herbaceous species which were severely damaged by an exposure to elevated ozone. Even so, after a six-week treatment with ozone genetic profiles did not reveal differences in community composition. However, some minor variations occurred in the intensities of three single bands in case of *Sonchus asper* (Dohrmann & Tebbe 2005). To increase the sensitivity of detection, genetic profiles representing Alphaproteobacteria, Actinobacteria and Pseudomonas were analysed separately in addition to those of Bacteria. The results of this study indicated that, even when the plants were visibly injured by ozone, the stress was not transmitted to the soil in a way that affected the structural diversity of the dominant rhizosphere bacterial community (Dohrmann & Tebbe 2006). However, in contrast to the studies reported above, here a short-term exposure was used suggesting that long-term observations are needed to follow the fate of soil microbial communities under slightly changed climate conditions.

Considering an agro-ecosystem, Chen et al. (2009) reported on a reduction in the functional richness of the soil microbial community in the rhizosphere of *T. aestivum*, with ozone concentrations above 110 ppb remarkably decreased the Shannon diversity index of soil microbial community function. Associated with ozone treated *Glycine max,* Pereira et al. (2011) reported on an increase in the soil bacterial abundance. By estimating the nitrous oxide reductase gene in soil they concluded that elevated ozone may decrease soil mineral N through a reduction in plant material input and increased denitrification. Similarly, He et al. (2014) related a shift in microbial communities beneath *G. max* to an inhibition of key functional genes involved in N processes of the soil caused by elevated ozone.

In a field with rice-wheat crop rotation the genotypic diversity and metabolic versatility of anoxygenic phototrophic purple bacteria associated with rice decreased in response to elevated ozone (Feng et al. 2011). In addition, it was shown that elevated ozone altered the composition of paddy methanogenic communities and reduced the abundance and diversity of paddy methanogens (Feng et al. 2013). As a consequence, the methanogenic activity was inhibited by elevated ozone. When sampled in association with wheat the fungal PLFA and the fungi - bacteria ratio decreased after exposure to ozone (Li et al. 2012) but overall functional structure of rhizosphere microbial communities did not significantly change (Li et al. 2013).

However, the abundance of specific functional genes involved in C fixation and degradation, nitrogen fixation, and sulfite reduction altered in response to ozone and differences between cultivars in relation to their ozone sensitivity were indicated (Li et al. 2012; Li et al. 2013).

5.4.4 Beneficial microbes

Some microbes are classified as beneficial ones because of their ability to help plants to deal with pathogens and herbivorous insects as well as to tolerate abiotic stress (Pineda et al. 2013). For example, the beneficial effect of mycorrhizal infection of soybeans with *Glomus geosporum* was also shown in terms of its capability to enhance the ozone tolerance of the host plant (Brewer & Heagle 1983). Similarly, plant growth-promoting rhizobacteria (*Bacillus subtilis*) protected *Pinus taeda* seedlings against both ozone effects, foliar injury and root growth reductions (Estes et al. 2004).

Because of its implication for nutrient acquisition and carbohydrate allocation the degree of mycorrhization and its modification by ozone is of high importance for the ecosystem. The host/fungal relationship and its response to stress is strongly linked to carbon allocation within the host plant (Andersen & Rygiewicz 1991). In contrast to its beneficial effect Andersen (2003) expected an increase in ozone sensitivity because mycorrhizal symbioses increase the sink strength of roots for carbon and thus may limit the availability of carbon for defence and repair. However, any disturbance in carbon allocation induced by ozone may in turn influence the carbon availability of the ectomycorrhizal fungus, which was demonstrated for *Pinus ponderosa* (Andersen & Rygiewicz 1995) and at the Aspen-FACE site (Andrew & Lilleskov 2009; Podila et al. 2011).

Several studies showed an increase in mycorrhizal abundance for tree species when exposed to ozone (reviewed by Andersen 2003). More recently, this was shown for example for *Betula pendula* (Kasurinen et al. 2005), *Populus tremuloides* (Andrew & Lilleskov 2009; Podila et al. 2011) hybrid aspen *P. tremula* x *P. tremuloides* (Haikio et al. 2009), and *Fagus sylvatica* (Grebenc & Kraigher 2007a; Pritsch et al. 2009). There is rising evidence that ozone may impact microbial diversity in terms of mycorrhizal colonisation of trees. Alteration in mycorrhizal species composition has been detected for *Pinus taeda* (Edwards & Kelly 1992), *Betula pendula* (Kasurinen et al. 2005), *Fagus sylvatica* (Grebenc & Kraigher 2007b; Haberer et al. 2007), and recently for the aspen-birch forest ecosystems (Edwards & Zak 2011). After 10 years of exposure Edwards & Zak (2011) concluded that in an aspen-birch forest ecosystem ozone seemed to have both a stimulatory and repressive effect depending on the soil horizon and time of examination.

Currently, there are limited data about the ozone effect on mycorrhization of grassland species. The mycorrhizal colonization of blue wildrye (*Elymus glaucus*) was reduced in response to ozone, however it was demonstrated that this effect depends on the genotype of the grass tested (Yoshida et al. 2001). From their review Cairney & Meharg (1999) deduced that different forms of pollution have been reported to alter the structure of below-ground communities of mycorrhizal fungi to some degree. They further concluded that to predict the consequences of such changes in mycorrhizal fungal communities a better understanding of the functional significance of mycorrhizal fungal diversity is needed.

5.4.5 Mesofauna community

Furthermore, to understand changes in structure and function of ecosystems, the potential impact on the activity of detritivore invertebrate communities should not be neglected. Currently, there are only a few studies published that show effects of elevated ozone on soil fauna. In a temperate forest soil (Aspen FACE) the individual density of soil mites (Acari) was reduced by nearly 50 % under elevated ozone conditions, whereas the collembolan abundances remained unaffected (Loranger et al. 2004). Feeding experiments with litter of changed quality due to its production under ozone exposure conditions were able to demonstrate that growth rates for earthworm were reduced when fed with birch litter (Kasurinen et al. 2007b) while litter of ozone treated aspen had no effect (Meehan et al. 2010), nevertheless it negatively affected the growth of springtails.

In agro-ecosystems significant decreases in the individual density of enchytraeids, collembolans and soil mites in the rhizosphere of ozone exposed wheat plants (Schrader et al. 2009) or a reduction of the abundance and diversity of Collembola associated with cotton plants (Chang et al. 2011) were reported, whereas the nematode diversity index decreased and nematode dominance index increased in association with ozone treated soybean (Bao et al. 2014).

5.4.6 Conclusion

In spite of the small number of studies, for microbial and invertebrate communities an influence on both the dynamic of decomposing nutrient cycling processes and the community composition by elevated ozone is indicated. In general, this effect seemed to be attributed to plant-mediated shifts in substrate balance. Although, effects on below-ground microbial processes are highly complex and results have shown to be rather inconsistent, it could be concluded that elevated levels of ozone have the potential *i.)* to affect leaf litter quality, *ii).* to alter short-term litter decomposition dynamics, *iii.)* to influence the microbial activity in a differentiated way and thus *iv.)* to alter microbial and mesofauna communities.

These changes may be interpreted as an indication of stressed soil conditions and degraded soil food web (Bao et al. 2014). However it remains unclear whether such changes will be sustained in the longer term. Furthermore, there is evidence that feedbacks between roots and soil microbial populations affect plant species diversity and community structure (Bever et al. 1997; van der Heijden et al. 1998).

5.5 References

Agrell, J., Kopper, B., McDonald, E. P. & Lindroth, R. L. (2005): CO2 and O-3 effects on host plant preferences of the forest tent caterpillar (Malacosoma disstria). Global Change Biology 11, 588-599.

Andersen, C. P. (2000): Ozone stress and changes below-ground: Linking root and soil processes. Phyton-Annales Rei Botanicae 40, 7-12.

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. & Rygiewicz, P. T. (1991): Stress interactions and mycorrhizal plant-response - understanding carbon allocation priorities. Environmental Pollution 73, 217-244.

Andersen, C. P. & Rygiewicz, P. T. (1995): Allocation of carbon in mycorrhizal Pinus ponderosa seedlings exposed to ozone. New Phytologist 131, 471-480.

Andersen, C. P. & Scagel, C. F. (1997): Nutrient availability alters belowground respiration of ozone-exposed ponderosa pine. Tree Physiology 17, 377-387.

Andersen, C. P. & Grulke, N. E. (2001): Complexities in understanding ecosystem response to ozone. Human and Ecological Risk Assessment 7, 1169-1182.

Andersen, C. P., Hogsett, W. E., Plocher, M., Rodecap, K. & Lee, E. H. (2001): Blue wild-rye grass competition increases the effect of ozone on ponderosa pine seedlings. Tree Physiology 21, 319-327.

Andrew, C. & Lilleskov, E. A. (2009): Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO2 and O-3. Ecology Letters 12, 813-822.

Aneja, M. K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J. C. & Schloter, M. (2007): Influence of ozone on litter quality and its subsequent effects on the initial structure of colonizing microbial communities. Microbial Ecology 54, 151-160.

Arndt, U. (1995): Air-pollutants and pheromones - A problem. Chemosphere 30, 1023-1031.

Ashburn, A. K. & Lindroth, R. L. (2001): Effects of elevated atmospheric carbon dioxide and ozone on canopy insect biodiversity. Ecological Society of America Annual Meeting Abstracts 86, 250.

Ashmore, M. R. & Ainsworth, N. (1995): The effects of ozone and cutting on the species composition of artificial grassland communities. Functional Ecology 9, 708-712.

Ashmore, M. R., Power, S. A., Cousins, D. A. & Ainsworth, N. (1996): Effects of Ozone on Native Grass and Forb Species: a Comparison of Responses of Individual Plants and Artificial Communities. Critical Levels for Ozone: Testing and Finalizing the Concepts UN-ECE Workshop Report (ed. by L. Kärenlampi &L. Skärby), pp. 193-197. Kuopio.

Ashmore, M. R., Thwaites, R. H., Ainsworth, N., Cousins, D. A., Power, S. A. & Morton, A. J. (1995): Effects of ozone on calcareous grassland communities. Water Air and Soil Pollution 85, 1527-1532.

Awmack, C. S., Harrington, R. & Lindroth, R. L. (2004): Aphid individual performance may not predict population responses to elevated CO2 or O-3. Global Change Biology 10, 1414-1423.

Awmack, C. S., Mondor, E. B. & Lindroth, R. L. (2007): Forest understory clover populations in enriched CO2 and O-3 atmospheres: Interspecific, intraspecific, and indirect effects. Environmental and Experimental Botany 59, 340-346.

Bahnweg, G., Heller, W., Stich, S., Knappe, C., Betz, G., Heerdt, C., Kehr, R. D., Ernst, D., Langebartels, C., Nunn, A. J., Rothenburger, J., Schubert, R., Wallis, P., Muller-Starck, G., Werner, H., Matyssek, R. & Sandermann, H. (2005): Beech leaf colonization by the endophyte Apiognomonia errabunda dramatically depends on light exposure and climatic conditions. Plant Biology 7, 659-669.

Baldantoni, D., Bellino, A., Manes, F. & Alfani, A. (2013): Ozone fumigation of Quercus ilex L. slows down leaf litter decomposition with no detectable change in leaf composition. Annals of Forest Science 70, 571-578.

Bandeff, J. M., Pregitzer, K. S., Loya, W. M., Holmes, W. E. & Zak, D. R. (2006): Overstory community composition and elevated atmospheric CO2 and O-3 modify understory biomass production and nitrogen acquisition. Plant and Soil 282, 251-259.

Bao, X. L., Li, Q., Hua, J. F., Zhao, T. H. & Liang, W. J. (2014): Interactive effects of elevated ozone and UV-B radiation on soil nematode diversity. Ecotoxicology 23, 11-20.

Barbo, D. N., Chappelka, A. H. & Stolte, K. W. (1995): Ozone effects on productivity and diversity of an early successional forest community. Bulletin of the Ecological Society of America 76 (2), Suppl. Part 2.

Barbo, D. N., Chappelka, A. H., Somers, G. L., Miller-Goodman, M. S. & Stolte, K. (1998): Diversity of an early successional plant community as influenced by ozone. New Phytologist 138, 653-662.

Barbo, D. N., Chappelka, A. H., Somers, G. L., Miller-Goodman, M. S. & Stolte, K. (2002): Ozone impacts on loblolly pine (Pinus taeda L.) grown in a competitive environment. Environmental Pollution 116, 27-36.

Bassin, S., Volk, M. & Fuhrer, J. (2007a): Factors affecting the ozone sensitivity of temperate European grasslands: An overview. Environmental Pollution 146, 678-691.

Bassin, S., Volk, M. & Fuhrer, J. (2013): Species Composition of Subalpine Grassland is Sensitive to Nitrogen Deposition, but Not to Ozone, After Seven Years of Treatment. Ecosystems 16, 1105-1117.

Bassin, S., Volk, M., Suter, M., Buchmann, N. & Fuhrer, J. (2007b): Nitrogen deposition but not ozone affects productivity and community composition of subalpine grassland after 3 yr of treatment. New Phytologist 175, 523-534.

Bassin, S., Werner, R. A., Sorgel, K., Volk, M., Buchmann, N. & Fuhrer, J. (2009): Effects of combined ozone and nitrogen deposition on the in situ properties of eleven key plant species of a subalpine pasture. Oecologia 158, 747-756.

Beare, J. A., Archer, S. A. & Bell, J. N. B. (1999a): Effects of Melampsora leaf rust disease and chronic ozone exposure on poplar. Environmental Pollution 105, 419-426.

Beare, J. A., Archer, S. A. & Bell, J. N. B. (1999b): Marssonina leafspot disease of poplar under elevated ozone: pre-fumigated host and in vitro studies. Environmental Pollution 105, 409-417.

Bender, J., Bergmann, E. & Weigel, H. J. (2003): Multi-year experiments on ozone effects on semi-natural vegetation: implications for the development of critical levels. In: Establishing Ozone Critical Levels II, UNECE Workshop Report. IVL report B 1523 (ed. by P. E. Karlsson, G.Selldén &H. Pleijel), Gothenburg, Sweden. pp. 211-217.

Bender, J., Muntifering, R. B., Lin, J. C. & Weigel, H. J. (2006): Growth and nutritive quality of Poa pratensis as influenced by ozone and competition. Environmental Pollution 142, 109-115.

Bender, J., Bergmann, E., Dohrmann, A., Tebbe, C. C. & Weigel, H. J. (2002): Impact of ozone on plant competition and structural diversity of rhizosphere microbial communities in grassland mesocosms. Phyton-Annales Rei Botanicae 42, 7-12.

Bennett, J. P. (1976): Effects of low levels of ozone on plant populations. Dissertation Abstracts International, B 36, 5944.

Bennett, J. P. & Runeckles, V. C. (1977): Effects of low-levels of ozone on plant competition. Journal of Applied Ecology 14, 877-880.

Bever, J. D., Westover, K. M. & Antonovics, J. (1997): Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85, 561-573.

Bidart-Bouzat, M. G. & Imeh-Nathaniel, A. (2008): Global Change Effects on Plant Chemical Defenses against Insect Herbivores. Journal of Integrative Plant Biology 50, 1339-1354.

Bilgin, D. D., Aldea, M., O'Neill, B. F., Benitez, M., Li, M., Clough, S. J. & DeLucia, E. H. (2008): Elevated ozone alters soybean-virus interaction. Molecular Plant-Microbe Interactions 21, 1297-1308.

Blum, U., Heagle, A. S., Burns, J. C. & Linthurst, R. A. (1983): The effects of ozone on fescue-clover forage - regrowth, yield and quality. Environmental and Experimental Botany 23, 121-132.

Boland, G. J., Melzer, M. S., Hopkin, A., Higgins, V. & Nassuth, A. (2004): Climate change and plant diseases in Ontario. Canadian Journal of Plant Pathology 26, 335-350.

Bonello, P., Heller, W. & Sandermann, H. (1993a): Ozone effects on root -disease susceptibility and defense responses in mycorrhizal and non-mycorrhizal seedlings of scots pine (Pinus sylvstris). New Phytologist 124, 653-663.

Bonello, P., Heller, W. & Sandermann, H., Jr. (1993b): Ozone effects on root-disease susceptibility and defence responses in mycorrhizal and non-mycorrhizal seedlings on Scots pine (Pinus sylvestris L.). New Phytologist 124, 653-663.

Braun, S. & Fluckiger, W. (1989): Effect of ambient ozone and acid mist on aphid development. Environmental Pollution 56, 177-188.

Brewer, P. F. & Heagle, A. S. (1983): Interactions between Glomus-geosporum and exposure of soybeans to ozone or simulated acid rain in the field. Phytopathology 73, 1035-1040.

Brown, V. C., McNeill, S. & Ashmore, M. R. (1992): The effects of ozone fumigation on the performance of the black bean aphid, Aphis fabae Scop., feeding on broad beans, Vicia faba L. Agriculture Ecosystems & Environment 38, 71-78.

Brown, V. C., Ashmore, M. R. & McNeill, S. (1993): Experimental investigations of the effects of air-pollutants on aphids on coniferous trees. Forstwissenschaftliches Centralblatt 112, 128-132.

Cairney, J. W. G. & Meharg, A. A. (1999): Influences of anthropogenic pollution on mycorrhizal fungal communities. Environmental Pollution 106, 169-182.

Cannon, W. N., Jr. (1993): Gypsy moth (Lepidoptera: Lymantriidae) consumption and utilization of northern red oak and white oak foliage exposed to simulated acid rain and ozone. Environmental Entomology 22, 669-673.

Carey, W. A. & Kelley, W. D. (1994): Interaction of ozone exposure and Fusarium subglutinans inoculation on growth and disease development of loblolly pine seedlings. Environmental Pollution 84, 35-43.

Chang, L. A., Liu, X. H. & Ge, F. (2011): Effect of elevated O-3 associated with Bt cotton on the abundance, diversity and community structure of soil Collembola. Applied Soil Ecology 47, 45-50.

Chen, Z., Wang, X. K., Feng, Z. Z., Xiao, Q. & Duan, X. N. (2009): Impact of elevated O-3 on soil microbial community function under wheat crop. Water Air and Soil Pollution 198, 189-198.

Chung, H. G., Zak, D. R. & Lilleskov, E. A. (2006): Fungal community composition and metabolism under elevated CO2 and O-3. Oecologia 147, 143-154.

Cobb, F. W. & Stark, R. W. (1970): Decline and mortality of smog-injured ponderosa pine. Journal of Forestry 68, 147-&.

Cobb, F. W., Wood, D. L., Stark, R. W. & Parmeter, J. R. (1968): Theory on relationships between oxidant injury and bark beetle infestation. Hilgardia 39, 141-152.

Coleman, M. D., Dickson, R. E. & Isebrands, J. G. (1996): Root growth and respiration of aspen in response to ozone and elevated carbon dioxide. In: 1995 Meeting of the Northern Global Change Program (ed. by J. Hom, R. Birdsey &K. Obrian), US Dept Agr, Forest, pp. 20-20.

Cornelius, R. & Markan, K. (1984): Interferenz von Urtica urens L: und Chenopodium album L. unter Ozoneinfluss - Effect of Ozone on the Interference of Urtica urens L. and Chenopodium L. . Angewandte Botanik 58, 195-206.

Costa, S. D., Kennedy, G. G. & Heagle, A. S. (2001): Effect of host plant ozone stress on Colorado potato beetles. Environmental Entomology 30, 824-831.

Couture, J. J., Meehan, T. D. & Lindroth, R. L. (2012): Atmospheric change alters foliar quality of host trees and performance of two outbreak insect species. Oecologia 168, 863-876.

Cui, H. Y., Sun, Y. C., Su, J. W., Ren, Q., Li, C. Y. & Ge, F. (2012): Elevated O-3 reduces the fitness of Bemisia tabaci via enhancement of the SA-dependent defense of the tomato plant. Arthropod-Plant Interactions 6, 425-437.

Dahlsten, D. L., Rowney, D. L. & Kickert, R. N. (1997): Effects of oxidant air pollutants on western pine beetle (Coleoptera: Scolytidae) populations in southern California. Environmental Pollution 96, 415-423.

Dermody, O., O'Neill, B. F., Zangerl, A. R., Berenbaum, M. R. & DeLucia, E. H. (2008): Effects of elevated CO2 and O-3 on leaf damage and insect abundance in a soybean agroecosystem. Arthropod-Plant Interactions 2, 125-135.

Dohrmann, A. B. & Tebbe, C. C. (2005): Effect of elevated tropospheric ozone on the structure of bacterial communities inhabiting the rhizosphere of herbaceous plants native to Germany. Applied and Environmental Microbiology 71, 7750-7758.

Dohrmann, A. B. & Tebbe, C. C. (2006): Genetic profiling of bacterial communities from the rhizospheres of ozone damaged Malva sylvestris (Malvaceae). European Journal of Soil Biology 42, 191-199.

Dunbar, J., Gallegos-Graves, L., Steven, B., Mueller, R., Hesse, C., Zak, D. R. & Kuske, C. R. (2014): Surface soil fungal and bacterial communities in aspen stands are resilient to eleven years of elevated CO2 and O-3. Soil Biology & Biochemistry 76, 227-234.

Eastburn, D. M., McElrone, A. J. & Bilgin, D. D. (2011): Influence of atmospheric and climatic change on plant-pathogen interactions. Plant Pathology 60, 54-69.

Eatough Jones, M. & Paine, T. D. (2006): Detecting changes in insect herbivore communities along a pollution gradient. Environmental Pollution 143, 377-387.

Eatough Jones, M., Paine, T. D., Fenn, M. E. & Poth, M. A. (2004): Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. Forest Ecology and Management 200, 67-76.

Edwards, G. S. & Kelly, J. M. (1992): Ectomycorrhizal colonization of loblolly-pine seedlings during 3 growing seasons in response to ozone, acidic precipitation, and soil Mg status. Environmental Pollution 76, 71-77.

Edwards, I. P. & Zak, D. R. (2011): Fungal community composition and function after long-term exposure of northern forests to elevated atmospheric CO2 and tropospheric O-3. Global Change Biology 17, 2184-2195.

Edwards, N. T. (1991): Root and soil respiration responses to ozone in Pinus taeda L. seedlings. New Phytologist 118, 315-321.

Endress, A. G. & Post, S. L. (1985): Altered feeding preference of Mexican bean beetle Epilachna varivestis for ozonated soybean foliage. Environmental Pollution, 39, 9-16.

Endress, A. G. & Iverson, L. R. (1999): Drought and ozone stress effects on competition among selected prairie grass species and giant foxtail. HortTechnology 9, 227-234.

Esperschutz, J., Pritsch, K., Gattinger, A., Welzl, G., Haesler, F., Buegger, F., Winkler, J. B., Munch, J. C. & Schloter, M. (2009): Influence of chronic ozone stress on carbon translocation pattern into rhizosphere microbial communities of beech trees (Fagus sylvatica L.) during a growing season. Plant and Soil 323, 85-95.

Estes, B. L., Enebak, S. A. & Chappelka, A. H. (2004): Loblolly pine seedling growth after inoculation with plant growth-promoting rhizobacteria and ozone exposure. Canadian Journal of Forest Research 34, 1410-1416.

Evans, P. A. & Ashmore, M. R. (1992): The Effects of Ambient Air on a Semi-natural Grassland Community. Agriculture Ecosystems & Environment 38, 91-97.

Feng, Y. Z., Lin, X. G., Yu, Y. C. & Zhu, J. G. (2011): Elevated Ground-Level O-3 Changes the Diversity of Anoxygenic Purple Phototrophic Bacteria in Paddy Field. Microbial Ecology 62, 789-799.

Feng, Y. Z., Lin, X. G., Yu, Y. C., Zhang, H. Y., Chu, H. Y. & Zhu, J. G. (2013): Elevated ground-level O-3 negatively influences paddy methanogenic archaeal community. Scientific Reports 3

Fenn, M. E., Dunn, P. H. & Wilborn, R. (1990): Black stain root disease in ozone-stressed ponderosa pine. Plant Disease 74, 426-430.

Fleischmann, F., Winkler, J. B. & Osswald, W. (2009): Effects of ozone and Phytophthora citricola on non-structural carbohydrates of European beech (Fagus sylvatica) saplings. Plant and Soil 323, 75-84.

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

Fuhrer, J. (1994): Effects of ozone on managed pasture .1. Effects of open-top chambers on microclimate, ozone flux, and plant-growth. Environmental Pollution 86, 297-305.

Fuhrer, J. (1997): Ozone sensitivity of managed pastures. In: Ecological Issues and Environmental Impact Assessment (ed. by P. N. Cheremisinoff), Gulf Publ Co, pp. 681-706.

Fuhrer, J., Shariatmadari, H., Perler, R., Tschannen, W. & Grub, A. (1994): Effects of ozone on managed pasture .2. Yield, species composition, canopy structure, and forage quality. Environmental Pollution 86, 307-314.

Gimeno, B. S., Bermejo, V., Sanz, J., de la Torre, D. & Gil, J. M. (2003): Ozone and competition adversely affect the reproductive ability of three clover species from Iberian rangelands. In: Establishing Ozone Critical Levels II, UNECE Workshop Report. IVL report B 1523 (ed. by P. E. Karlsson, G. Selldén &H. Pleijel), Gothenburg, Sweden pp. 218-223.

González-Fernández, I., Bass, D., Muntifering, R., Mills, G. & Barnes, J. (2008): Impacts of ozone pollution on productivity and forage quality of grass/clover swards. Atmospheric Environment 42, 8755-8769.

Grams, T. E. E. & Matyssek, R. (2010): Stable isotope signatures reflect competitiveness between trees under changed CO2/O-3 regimes. Environmental Pollution 158, 1036-1042.

Grams, T. E. E., Kozovits, A. R., Reiter, I. M., Winkler, J. B., Sommerkorn, M., Blaschke, H., Haberle, K. H. & Matyssek, R. (2002): Quantifying competitiveness in woody plants. Plant Biology 4, 153-158.

Grantz, D. A. & Shrestha, A. (2005): Ozone reduces crop yields and alters competition with weeds such as yellow nutsedge. California Agriculture 59, 137-143.

Grantz, D. A. & Shrestha, A. (2006): Tropospheric ozone and interspecific competition between yellow nutsedge and pima cotton. Crop Science 46, 1879-1889.

Grantz, D. A., Shrestha, A. & Vu, H. B. (2010): ozone impacts on assimilation and allocation to reproductive sinks in the vegetatively propagated C-4 weed, yellow nutsedge. Crop Science 50, 246-252.

Grebenc, T. & Kraigher, H. (2007a): Changes in the community of ectomycorrhizal fungi and increased fine root number under adult beech trees chronically fumigated with double ambient ozone concentration. Plant Biology 9, 279-287.

Grebenc, T. & Kraigher, H. (2007b): Types of ectomycorrhiza of mature beech and spruce at ozone-fumigated and control forest plots. Environmental Monitoring and Assessment 128, 47-59.

Grodzki, W., McManus, M., Knizek, M., Meshkova, V., Mihalciuc, V., Novotny, J., Turcani, M. & Slobodyan, Y. (2004): Occurrence of spruce bark beetles in forest stands at different levels of air pollution stress. Environmental Pollution 130, 73-83.

Grulke, N. E. & Lee, E. H. (1997): Assessing visible ozone-induced foliar injury in ponderosa pine. Canadian Journal of Forest Research 27, 1658-1668.

Haberer, K., Grebenc, T., Alexou, M., Gessler, A., Kraigher, H. & Rennenberg, H. (2007): Effects of long-term free-air ozone fumigation on delta N-15 and total N in Fagus sylvatica and associated mycorrhizal fungi. Plant Biology 9, 242-252.

Haikio, 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.

Hain, F. P. (1987): Interactions of insects, trees and air pollutants. Tree Physiology 3, 93-102.

Haldemann, C. & Fuhrer, J. (2005): Interactive effects of CO 2 and O 3 on the growth of Trisetum falvescens and Trifolium pratense grown in monoculture or a bi-species mixture. Journal of Crop Improvement 13, 275-289.

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. & Ashmore, M. (2010a): How much does the presence of a competitor modify the within-canopy distribution of ozone-induced senescence and visible injury? Water Air and Soil Pollution 210, 265-276.

Hayes, F., Williamson, J. & Mills, G. (2012): Ozone pollution affects flower numbers and timing in a simulated BAP priority calcareous grassland community. Environmental Pollution 163, 40-47.

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

Hayes, F., Mills, G., Harmens, H. & Wyness, K. (2011): Within season and carry-over effects following exposure of grassland species mixtures to increasing background ozone. Environmental Pollution 159, 2420-2426.

He, Z. L., Xiong, J. B., Kent, A. D., Deng, Y., Xue, K., Wang, G. J., Wu, L. Y., Van Nostrand, J. D. & Zhou, J. Z. (2014): Distinct responses of soil microbial communities to elevated CO2 and O-3 in a soybean agro-ecosystem. Isme Journal 8, 714-726.

Heagle, A. S., Brandenburg, R. L., Burns, J. C. & Miller, J. E. (1994): Ozone and carbon dioxide effects on spider mites in white clover and peanut. Journal of Environmental Quality 23, 1168-1176.

Heagle, A. S., Rebbeck, J., Shafer, S. R., Blum, U. & Heck, W. W. (1989): Effects of long-term ozone exposure and soil-moisture deficit on growth of a ladino clover tall fescue pasture. Phytopathology 79, 128-136.

Hillstrom, M. L. & Lindroth, R. L. (2008): Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. Insect Conservation and Diversity 1, 233-241.

Hillstrom, M. L., Vigue, L. M., Coyle, D. R., Raffa, K. F. & Lindroth, R. L. (2010): Performance of the invasive weevil Polydrusus sericeus is influenced by atmospheric CO2 and host species. Agricultural and Forest Entomology 12, 285-292.

Holopainen, J. K. (2002): Aphid response to elevated ozone and CO2. Entomologia Experimentalis et Applicata 104, 137-142.

Holopainen, J. K. & Kossi, S. (1998): Variable growth and reproduction response of the spruce shoot aphid, Cinara pilicornis, to increasing ozone concentrations. Entomologia Experimentalis et Applicata 87, 109-113.

Holopainen, J. K., Kainulainen, P. & Oksanen, J. (1997): Growth and reproduction of aphids and levels of free amino acids in Scots pine and Norway spruce in an open-air fumigation with ozone. Global Change Biology 3, 139-147.

Holopainen, J. K., Mustaniemi, A., Kainulainen, P. & Oksanen, J. (1992): Reproduction of aphids and spider mites and levels of amino acids in conifer seedlings exposed to ozone. In: Responses of forest ecosystems to environmental changes. Proceedings of the First European Symposium on Terrestrial Ecosystems, Forests and Woodland, pp. 965-966.

Holton, K. & Lindroth, R. L. (2001): Effects of elevated atmospheric CO2 and O3 on tree-insect-parasitoid interactions. Ecological Society of America Annual Meeting Abstracts 86, 294.

Holton, M. K., Lindroth, R. L. & Nordheim, E. V. (2003): Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO2, O-3, and plant genotype. Oecologia 137, 233-244.

Hummel, R. L., Brandenburg, R. L., Heagle, A. S. & Arellano, C. (1998): Effects of ozone on reproduction of twospotted spider mite (Acari : Tetranychidae) on white clover. Environmental Entomology 27, 388-394.

Jackson, D. M., Heagle, A. S. & Eckel, R. V. W. (1999): Ovipositional response of tobacco hornworm moths (Lepidoptera: Sphyngidae) to tobacco plants grown under elevated levels of ozone. Environmental Entomology 28, 566-571.

Jackson, D. M., Rufty, T. W., Heagle, A. S., Severson, R. F. & Eckel, R. V. W. (2000): Survival and development of tobacco hornworm larvae on tobacco plants grown under elevated levels of ozone. Journal of Chemical Ecology 26, 1-19.

Jackson, G. E. (1995): The effect of ozone, nitrogen dioxide or nitric oxide fumigation of cereals on the rose grain aphid meopolophium dirhodum. Agriculture Ecosystems & Environment 54, 187-194.

Jäggi, M., Ammann, C., Neftel, A. & Fuhrer, J. (2006): Environmental control of profiles of ozone concentration in a grassland canopy. Atmospheric Environment 40, 5496-5507.

James, R. L., Cobb, F. W., Wilcox, W. W. & Rowney, D. L. (1980a): Effects of photochemical oxidant injury of ponderosa and jeffrey pines on susceptibility of sapwood and freshly cut stumps to Fomes-annosus. Phytopathology 70, 704-708.

James, R. L., Cobb, F. W., Jr., Miller, P. R. & Parmeter, J. R., Jr. (1980b): Effects of oxidant air pollution on susceptibility of pine roots to Fomes annosus. Phytopathology 70, 560-563.

Jeffords, M. R. & Endress, A. G. (1984): Possible role of ozone in tree defoliation by the gypsy moth Lymantria-dispar lepidoptera Lymantriidae. Environmental Entomology 13, 1249-1252.

Johnson, B. G., Hale, B. A. & Ormrod, D. P. (1996): Carbon dioxide and ozone effects on growth of a legume-grass mixture. Journal of Environmental Quality 25, 908-916.

Kainulainen, P., Holopainen, J. K. & Holopainen, T. (2000): Combined effects of ozone and nitrogen on secondary compounds, amino acids, and aphid performance in Scots pine. Journal of Environmental Quality 29, 334-342.

Kainulainen, P., Holopainen, J. K., Hyttinen, H. & Oksanen, J. (1994): Effect of ozone on the biochemistry and aphid infestation of Scots pine. Phytochemistry (Oxford) 35, 39-42.

Kanerva, T., Palojärvi, A., Rämö, K. & Manninen, S. (2008): Changes in soil microbial community structure under elevated tropospheric O-3 and CO2. Soil Biology & Biochemistry 40, 2502-2510.

Kanerva, T., Regina, K., Rämö, K., Ojanperä, K. & Manninen, S. (2007): Fluxes of N2O, CH4 and CO2 in a meadow ecosystem exposed to elevated ozone and carbon dioxide for three years. Environmental Pollution 145, 818-828.

Karnosky, D. F., Percy, K. E., Xiang, B. X., Callan, B., Noormets, A., Mankovska, B., Hopkin, A., Sober, J., Jones, W., Dickson, R. E. & Isebrands, J. G. (2002): Interacting elevated CO2 and tropospheric O-3 predisposes aspen (Populus tremuloides Michx.) to infection by rust (Melampsora medusae f. sp tremuloidae). Global Change Biology 8, 329-338.

Kasurinen, A., Kokko-Gonzales, P., Riikonen, J., Vapaavuori, E. & Holopainen, T. (2004): Soil CO2 efflux of two silver birch clones exposed to elevated CO2 and O-3 levels during three growing seasons. Global Change Biology 10, 1654-1665.

Kasurinen, A., Riikonen, J., Oksanen, E., Vapaavuori, E. & Holopainen, T. (2006): Chemical composition and decomposition of silver birch leaf litter produced under elevated CO2 and O-3. Plant and Soil 282, 261-280.

Kasurinen, A., Peltonen, P., Holopainen, J. K., Vapaavuori, E. & T., H. (2007a): Leaf litter under changing climate: will increasing levels of CO2 and O3 affect decomposition and nutrient cycling processes? In: Dynamic Soil, Dynamic Plant Global Science Books, pp. 58-67.

Kasurinen, A., Keinanen, M. M., Kaipainen, S., Nilsson, L. O., Vapaavuori, E., Kontro, M. H. & Holopainen, T. (2005): Below-ground responses of silver birch trees exposed to elevated CO2 and O-3 levels during three growing seasons. Global Change Biology 11, 1167-1179.

Kasurinen, A., Peltonen, P. A., Julkunen-Tiitto, R., Vapaavuori, E., Nuutinen, V., Holopainen, T. & Holopainen, J. K. (2007b): Effects of elevated CO2 and O-3 on leaf litter phenolics and subsequent performance of litter-feeding soil macrofauna. Plant and Soil 292, 25-43.

Kelting, D. L., Burger, J. A. & Edwards, G. S. (1995): The effects of ozone on the root dynamics of seedlings and mature red oak (Quercus rubra L). Forest Ecology and Management 79, 197-206.

Khan, M. R. & Khan, M. W. (1998): Interactive effects of ozone and root-knot nematode on tomato. Agriculture Ecosystems & Environment 70, 97-107.

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.

King, J. S., Pregitzer, K. S., Zak, D. R., Sober, J., Isebrands, J. G., Dickson, R. E., Hendrey, G. R. & Karnosky, D. F. (2001): Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO-2 and tropospheric O-3. Oecologia 128, 237-250.

Klumpp, A., Bauer, E., Huttenlocher, F., Veit, U. & Gonschorrek, J. (1999): Effects of realistic ozone concentrations on the sex pheromone of the green oak tortrix (Tortrix viridana L.). In: Communications of the German Society for General and Applied Entomology, Vol 12, Nos 1-6, Feb 2000 (ed. by D. Mossakowski), pp. 67-70.

Kochhar, M., Blum, U. & Reinert, R. A. (1980): Effects of O3 and (or) fescue on ladino clover - interactions. Canadian Journal of Botany 58, 241-249.

Kochhar, M., Reinert, R. A. & Blum, U. (1982): Effects of fescue Festuca arundinacea and/or clover Trifolium repens debris and fescue leaf leachate on clover as modified by ozone and Rhizoctonia solani. Environmental Pollution 28, 255-264.

Kopper, B. J. & Lindroth, R. L. (2003a): Responses of trembling aspen (Populus tremuloides) phytochemistry and aspen blotch leafminer (Phyllonorycter tremuloidiella) performance to elevated levels of atmospheric CO2 and O-3. Agricultural and Forest Entomology 5, 17-26.

Kopper, B. J. & Lindroth, R. L. (2003b): Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore. Oecologia 134, 95-103.

Kozovits, A. R., Matyssek, R., Blaschke, H., Gottlein, A. & Grams, T. E. E. (2005a): Competition increasingly dominates the responsiveness of juvenile beech and spruce to elevated CO2 and/or O-3 concentrations throughout two subsequent growing seasons. Global Change Biology 11, 1387-1401.

Kozovits, A. R., Matyssek, R., Winkler, J. B., Gottlein, A., Blaschke, H. & Grams, T. E. E. (2005b): Above-ground space sequestration determines competitive success in juvenile beech and spruce trees. New Phytologist 167, 181-196.

Krupa, S., McGrath, M. T., Andersen, C. P., Booker, F. L., Burkey, K. O., Chappelka, A. H., Chevone, B. I., Pell, E. J. & Zilinskas, B. A. (2001): Ambient ozone and plant health. Plant Disease 85, 4-12.

Krupa, S. V. & Manning, W. J. (1988): Atmospheric Ozone: Formation and Effects on Vegetation. Environmental Pollution 50, 101-137.

Kubiske, M. E., Quinn, V. S., Marquardt, P. E. & Karnosky, D. F. (2007): Effects of elevated atmospheric CO(2) and/or O(3) on intra- and interspecific competitive ability of aspen. Plant Biology 9, 342-355.

Larson, J. L., Zak, D. R. & Sinsabaugh, R. L. (2002): Extracellular enzyme activity beneath temperate trees growing under elevated carbon dioxide and ozone. Soil Science Society of America Journal 66, 1848-1856.

Leininger, T. D., Winner, W. E. & Alexander, S. A. (1990): Root disease incidence in eastern white pine plantations with and without symptoms of ozone injury in the Coweeta basin of North Carolina USA. Plant Disease 74, 552-554.

Li, Q., Bao, X. L., Lu, C. Y., Zhang, X. K., Zhu, J. G., Jiang, Y. & Liang, W. J. (2012): Soil microbial food web responses to free-air ozone enrichment can depend on the ozone-tolerance of wheat cultivars. Soil Biology & Biochemistry 47, 27-35.

Li, X. Y., Deng, Y., Li, Q., Lu, C. Y., Wang, J. J., Zhang, H. W., Zhu, J. G., Zhou, J. H. & He, Z. L. (2013): Shifts of functional gene representation in wheat rhizosphere microbial communities under elevated ozone. Isme Journal 7, 660-671.

Lin, J. C., Nadarajah, K., Volk, M., Muntifering, R. B. & Fuhrer, J. (2007): Nutritive quality of a species-rich, extensively managed pasture exposed to elevated ozone in a free-air fumigation system. Journal of Animal Science 85, 37-37.

Liu, L. L., King, J. S. & Giardina, C. P. (2005): Effects of elevated concentrations of atmospheric CO2 and tropospheric O-3 on leaf litter production and chemistry in trembling aspen and paper birch communities. Tree Physiology 25, 1511-1522.

Liu, L. L., King, J. S. & Giardina, C. P. (2007): Effects of elevated atmospheric CO2 and tropospheric O-3 on nutrient dynamics: decomposition of leaf litter in trembling aspen and paper birch communities. Plant and Soil 299, 65-82.

Liu, L. L., King, J. S., Giardina, C. P. & Booker, F. L. (2009): The influence of chemistry, production and community composition on leaf litter decomposition under elevated atmospheric CO2 and tropospheric O-3 in a northern hardwood ecosystem. Ecosystems 12, 401-416.

Liu, W. P., Kozovits, A. R., Grams, T. E. E., Blaschke, H., Rennenberg, H. & Matyssek, R. (2004): Competition modifies effects of enhanced ozone/carbon dioxide concentrations on carbohydrate and biomass accumulation in juvenile Norway spruce and European beech. Tree Physiology 24, 1045-1055.

Loranger, G. I., Pregitzer, K. S. & King, J. S. (2004): Elevated CO2 and O-3 concentrations differentially affect selected groups of the fauna in temperate forest soils. Soil Biology & Biochemistry 36, 1521-1524.

Luedemann, G., Matyssek, R., Fleischmann, F. & Grams, T. E. E. (2005): Acclimation to ozone affects host/pathogen interaction and competitiveness for nitrogen on juvenile Fagus sylvatica and Picea abies trees infected with Phytophthora citricola. Plant Biology 7, 640-649.

Luedemann, G., Matyssek, R., Winkler, J. B. & Grams, T. E. E. (2009): Contrasting ozone x pathogen interaction as mediated through competition between juvenile European beech (Fagus sylvatica) and Norway spruce (Picea abies). Plant and Soil 323, 47-60.

Mainiero, R., Kazda, M., Haberle, K. H., Nikolova, P. S. & Matyssek, R. (2009): Fine root dynamics of mature European beech (Fagus sylvatica L.) as influenced by elevated ozone concentrations. Environmental Pollution 157, 2638-2644.

Manninen, A. M., Holopainen, T., Lyytikainen-Saarenmaa, P. & Holopainen, J. K. (2000): The role of low-level ozone exposure and mycorrhizas in chemical quality and insect herbivore performance on Scots pine seedlings. Global Change Biology 6, 111-121.

Manninen, S., Kanerva, T. & Rämö, K. (2005): Above- and below-ground responses of semi-natural vegetation to O3. In: Critical Levels of Ozone: Further Applying and Developing the Flux-based Concept (ed. by G. Wieser &M. Tausz), Obergurgl, Austria pp. 127-132.

Manninen, S., Aaltonen, H., Kanerva, T., Rämö, K. & Palojärvi, A. (2010): Plant and soil microbial biomasses in Agrostis capillaris and Lathyrus pratensis monocultures exposed to elevated O-3 and CO2 for three growing seasons. Soil Biology & Biochemistry 42, 1967-1975.

Manning, W. J. & von Tiedemann, A. (1995): Climate-change - potential effects of increased atmospheric carbon-dioxide (CO2), ozone (O-3), and ultraviolet-b (UV-b) radiation on plant-diseases. Environmental Pollution 88, 219-245.

McDonald, E. P., Kruger, E. L., Riemenschneider, D. E. & Isebrands, J. G. (2002): Competitive status influences tree-growth responses to elevated CO2 and O-3 in aggrading aspen stands. Functional Ecology 16, 792-801.

Meehan, T. D., Crossley, M. S. & Lindroth, R. L. (2010): Impacts of elevated CO2 and O-3 on aspen leaf litter chemistry and earthworm and springtail productivity. Soil Biology & Biochemistry 42, 1132-1137.

Menendez, A. I., Romero, A. M., Folcia, A. M. & Martinez-Ghersa, M. A. (2009): Getting the interactions right: Will higher O-3 levels interfere with induced defenses to aphid feeding? Basic and Applied Ecology 10, 255-264.

Miller, P. R. (1985): Ozone effects in the San Bernardino National Forest. In: Air pollution and the productivity of the forest. Symposium held Washington, DC, Oct. 4 and 5, 1983 (ed. by D. D. Davis, A. A. Millen &L. Dochinger), pp. 161-197.

Mina, U., Bhatia, A. & Kumar, U. (2012a): Response of maize and its pest Chilo partellus to ozone and carbon dioxide exposure. Maydica 57, 183-187.

Mina, U., Bhatia, A., Chakrabarti, B., Harit, R. C. & Kumar, U. (2012b): Impact of ozone and carbon dioxide on growth and development of Chilo partellus Swinhoe (maize stalk borer). Journal of Entomological Research (New Delhi) 36, 363-366.

Mondor, E. B., Tremblay, M. N., Awmack, C. S. & Lindroth, R. L. (2005): Altered genotypic and phenotypic frequencies of aphid populations under enriched CO(2) and O(3) atmospheres. Global Change Biology 11, 1990-1996.

Montes, R. A., Blum, U. & Heagle, A. S. (1982): The effects of ozone and nitrogen-fertilizer on tall fescue, ladino clover, and a fescue-clover mixture.1. Growth, regrowth, and forage production. Canadian Journal of Botany 60, 2745-2752.

Morsky, 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.

Nebel, B. & Fuhrer, J. (1994): Interspecific and intraspecific differences in ozone sensitivity in seminatural plant-communities. Angewandte Botanik 68, 116-121.

Nikolova, P. S., Andersen, C. P., Blaschke, H., Matyssek, R. & Haberle, K. H. (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.

Nussbaum, S., Geissmann, M. & Fuhrer, J. (1995): Ozone exposure-response relationships for mixtures of perennial ryegrass and white clover depend on ozone exposure patterns. Atmospheric Environment 29, 989-995.

Nussbaum, S., Bungener, P., Geissmann, M. & Fuhrer, J. (2000): Plant-plant interactions and soil moisture might be important in determining ozone impacts on grasslands. New Phytologist 147, 327-335.

Nygaard, P. H. (1994): Effects of ozone on Vaccinium myrtillus, Hylocomium splendens, Pleurozium schreberi and Dicranum polysetum. In: Rapport fra Skogforsk, pp. 1-17.

O'Neill, B. F., Zangerl, A. R., Delucia, E. H. & Berenbaum, M. R. (2008): Longevity and fecundity of Japanese beetle (Popillia japonica) on foliage grown under elevated carbon dioxide. Environmental Entomology 37, 601-607.

Olbrich, M., Knappe, C., Wenig, M., Gerstner, E., Haberle, K. H., Kitao, M., Matyssek, R., Stich, S., Leuchner, M., Werner, H., Schlink, K., Muller-Starck, G., Welzl, G., Scherb, H., Ernst, D., Heller, W. & Bahnweg, G. (2010): Ozone fumigation (twice ambient) reduces leaf infestation following natural and artificial inoculation by the endophytic fungus Apiognomonia errabunda of adult European beech trees. Environmental Pollution 158, 1043-1050.

Olszyk, D. M., Johnson, M. G., Phillips, D. L., Seidler, R. J., Tingey, D. T. & Watrud, L. S. (2001): Interactive effects of CO2 and O-3 on a ponderosa pine plant/litter/soil mesocosm. Environmental Pollution 115, 447-462.

Parsons, W. F. J., Lindroth, R. L. & Bockheim, J. G. (2004): Decomposition of Betula papyrifera leaf litter under the independent and interactive effects of elevated CO2 and O-3. Global Change Biology 10, 1666-1677.

Parsons, W. F. J., Bockheim, J. G. & Lindroth, R. L. (2008): Independent, interactive, and species-specific responses of leaf litter decomposition to elevated CO(2) and O(3) in a northern hardwood forest. Ecosystems 11, 505-519.

Pearce, R. B. (1996): Effects of exposure to high ozone concentrations on stilbenes in Sitka spruce (Picea sitchensis (Bong) Carr) bark and on its lignification response to infection with Heterobasidion annosum (Fr) Bref. Physiological and Molecular Plant Pathology 48, 117-129.

Pearce, R. B. & McLeod, A. R. (1995): Effects of sulphur dioxide and ozone on stilbenes and disease resistance in spruce trees from the Liphook Forest Fumigation Project. Plant Cell and Environment 18, 303-307.

Percy, K. E., Mankovska, B., Hopkin, A., Callan, B. & Karnosky, D. F. (2003): Ozone affects leaf surface-pest interactions. In: Air Pollution, Global Change and Forests in the New Millennium (ed. by D. F. Karnosky, K. E. Percy et al.), Elsevier, pp. 247-258.

Pereira, E. I. P., Chung, H., Scow, K., Sadowsky, M. J., van Kessel, C. & Six, J. (2011): Soil nitrogen transformations under elevated atmospheric CO2 and O-3 during the soybean growing season. Environmental Pollution 159, 401-407.

Pfleeger, T. G., da Luz, M. A. & Mundt, C. C. (1999): Lack of a synergistic interaction between ozone and wheat leaf rust in wheat swards. Environmental and Experimental Botany 41, 195-207.

Pfleeger, T. G., Plocher, M. & Bichel, P. (2010): Response of pioneer plant communities to elevated ozone exposure. Agriculture Ecosystems & Environment 138, 116-126.

Pineda, A., Dicke, M., Pieterse, C. M. J. & Pozo, M. J. (2013): Beneficial microbes in a changing environment: are they always helping plants to deal with insects? Functional Ecology 27, 574-586.

Pleijel, H., Karlsson, G. P., Sild, E., Danielsson, H., Skärby, L. & Sellden, G. (1996): Exposure of a grass-clover mixture to ozone in open-top chambers - Effects on yield, quality and botanical composition. Agriculture Ecosystems & Environment 59, 55-62.

Plessl, M., Elstner, E. F., Rennenberg, H., Habermeyer, J. & Heiser, I. (2007): Influence of elevated CO(2) and ozone concentrations on late blight resistance and growth of potato plants. Environmental and Experimental Botany 60, 447-457.

Plessl, M., Heller, W., Payer, H. D., Elstner, E. F., Habermeyer, J. & Heiser, I. (2005): Growth parameters and resistance against Drechslera teres of spring barley (Hordeum vulgare L. cv. Scarlett) grown at elevated ozone and carbon dioxide concentrations. Plant Biology (Stuttgart) 7, 694-705.

Podila, G. K., Miller, R. M., Cseke, L. J., White, H. L. & Allison, V. (2011): Ecogenomics of mycorrhizal interactions mediated by the aspen genome under elevated ozone and carbon dioxide.

Pregitzer, K., Loya, W., Kubiske, M. & Zak, D. (2006): Soil respiration in northern forests exposed to elevated atmospheric carbon dioxide and ozone. Oecologia 148, 503-516.

Pregitzer, K. S., Burton, A. J., King, J. S. & Zak, D. R. (2008): Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO-2 and tropospheric O-3. New Phytologist 180, 153-161.

Pretzsch, H. & Schutze, G. (2009): Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. European Journal of Forest Research 128, 183-204.

Pretzsch, H., Dieler, J., Matyssek, R. & Wipfler, P. (2010): Tree and stand growth of mature Norway spruce and European beech under long-term ozone fumigation. Environmental Pollution 158, 1061-1070.

Pritsch, K., Esperschuetz, J., Haesler, F., Raidl, S., Winkler, B. & Schloter, M. (2009): Structure and activities of ectomycorrhizal and microbial communities in the rhizosphere of Fagus sylvatica under ozone and pathogen stress in a lysimeter study. Plant and Soil 323, 97-109.

Rämö, K., Kanerva, T., Ojanperä, K. & Manninen, S. (2007): Growth onset, senescence, and reproductive development of meadow species in mesocosms exposed to elevated O-3 and CO2. Environmental Pollution 145, 850-860.

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

Rebbeck, J., Blum, U. & Heagle, A. S. (1988): Effects of ozone on the regrowth and energy reserves of a ladino clover tall fescue pasture. Journal of Applied Ecology 25, 659-681.

Renaud, J. P., Allard, G. & Mauffette, Y. (1997): Effects of ozone on yield, growth, and root starch concentrations of two alfalfa (Medicago sativa L) cultivars. Environmental Pollution 95, 273-281.

Rodenkirchen, H., Gottlein, A., Kozovits, A. R., Matyssek, R. & Grams, T. E. E. (2009): Nutrient contents and efficiencies of beech and spruce saplings as influenced by competition and O-3/CO2 regime. European Journal of Forest Research 128, 117-128.

Rusch, H. & Laurence, J. A. (1993): Interactive effects of ozone and powdery mildew on pea seedlings. Phytopathology 83, 1258-1263.

Rust, S. & Roloff, A. (2009): Competition in mixed stands of beech and spruce: effects of climate and ozone. European Journal of Forest Research 128, 85-86.

Sah, D. N., von Tiedemann, A. & Fehrmann, H. (1993): Effects of ozone exposure on resistance of wheat genotypes to Pyrenophora-tritici-repentis. Journal of Phytopathology-Phytopathologische Zeitschrift 138, 249-256.

Sandermann, H. (2000): Ozone/biotic disease interactions: molecular biomarkers as a new experimental tool. Environmental Pollution 108, 327-332.

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.

Scebba, F., Canaccini, F., Castagna, A., Bender, J., Weigel, H. J. & Ranieri, A. (2006): Physiological and biochemical stress responses in grassland species are influenced by both early-season ozone exposure and interspecific competition. Environmental Pollution 142, 540-548.

Schloter, M., Winkler, J. B., Aneja, M., Koch, N., Fleischmann, F., Pritsch, K., Heller, W., Stich, S., Grams, T. E. E., Gottlein, A., Matyssek, R. & Munch, J. C. (2005): Short term effects of ozone on the plant-rhizosphere-bulk soil system of young beech trees. Plant Biology 7, 728-736.

Schrader, S., Bender, J. & Weigel, H. J. (2009): Ozone exposure of field-grown winter wheat affects soil mesofauna in the rhizosphere. Environmental Pollution 157, 3357-3362.

Schulte, M. J. D., Matyssek, R., Gayler, S., Priesack, E. & Grams, T. E. E. (2013): Mode of competition for light and water amongst juvenile beech and spruce trees under ambient and elevated levels of O-3 and CO2. Trees-Structure and Function 27, 1763-1773.

Shrestha, A. & Grantz, D. A. (2005): Ozone impacts on competition between tomato and yellow nutsedge: Above- and below-ground effects. Crop Science 45, 1587-1595.

Stampfli, A. & Fuhrer, J. (2010): Spatial heterogeneity confounded ozone-exposure experiment in semi-natural grassland. Oecologia 162, 515-522.

Stark, R. W., Miller, P. R., Cobb, F. W., Wood, D. L. & Parmeter, J. R. (1968): Incidence of bark beetle infestation in injured trees. Hilgardia 39, 121-.

Steubing, L., Fangmeier, A., Both, R. & Frankenfeld, M. (1989): Effects of SO2, NO2, and O3 on population development and morphological and physiological-parameters of native herb layer species in a beech forest. Environmental Pollution 58, 281-302.

Stoelken, G., Pritsch, K., Simon, J., Mueller, C. W., Grams, T. E. E., Esperschuetz, J., Gayler, S., Buegger, F., Brueggemann, N., Meier, R., Zeller, B., Winkler, J. B. & Rennenberg, H. (2010): Enhanced ozone exposure of European beech (Fagus sylvatica) stimulates nitrogen mobilization from leaf litter and nitrogen accumulation in the soil. Plant Biosystems 144, 537-546.

Summers, C. G., Retzlaff, W. A. & Stephenson, S. (1994): The effect of ozone on the mean relative growth-rate of Diuraphis-noxia (Mordvilko) (Homoptera, Aphididae). Journal of Agricultural Entomology 11, 181-187.

Thwaites, R. H., Ashmore, M. R., Morton, A. J. & Pakeman, R. J. (2006): The effects of tropospheric ozone on the species dynamics of calcareous grassland. Environmental Pollution 144, 500-509.

Tingey, D. T., Johnson, M. G., Lee, E. H., Wise, C., Waschmann, R., Olszyk, D. M., Watrud, L. S. & Donegan, K. K. (2006): Effects of elevated CO2 and O-3 on soil respiration under ponderosa pine. Soil Biology & Biochemistry 38, 1764-1778.

Tonneijck, A. E. G. & Leone, G. (1993): Changes in susceptibility of bean-leaves (Phaseolus-vulgaris) to Sclerotinia-sclerotiorum and Botrytis-cinerea by pre-inoculative ozone exposures. Netherlands Journal of Plant Pathology 99, 313-322.

Tonneijck, A. E. G., Franzaring, J., Brouwer, G., Metselaar, K. & Dueck, T. A. (2004): Does interspecific competition alter effects of early season ozone exposure on plants from wet grasslands? Results of a three-year experiment in open-top chambers. Environmental Pollution 131, 205-213.

Trumble, J. T., Hare, J. D., Musselman, R. C. & McCool, P. M. (1987): Ozone-induced changes in host-plant suitability - interactions of Keiferia-lycopersicella and Lycopersicon-esculentum. Journal of Chemical Ecology 13, 203-218.

Valkama, E., Koricheva, J. & Oksanen, E. (2007): Effects of elevated O-3, alone and in combination with elevated CO2, on tree leaf chemistry and insect herbivore performance: a meta-analysis. Global Change Biology 13, 184-201.

van der Heijden, M. G. A., Boller, T., Wiemken, A. & Sanders, I. R. (1998): Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79, 2082-2091.

Vigue, L. M. & Lindroth, R. L. (2010): Effects of genotype, elevated CO2 and elevated O-3 on aspen phytochemistry and aspen leaf beetle Chrysomela crotchi performance. Agricultural and Forest Entomology 12, 267-276.

Volk, M., Geissmann, M., Blatter, A., Contat, F. & Fuhrer, J. (2003): Design and performance of a free-air exposure system to study long-term effects of ozone on grasslands. Atmospheric Environment 37, 1341-1350.

Volk, M., Bungener, P., Contat, F., Montani, M. & Fuhrer, J. (2006): Grassland yield declined by a quarter in 5 years of free-air ozone fumigation. Global Change Biology 12, 74-83.

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.

von Tiedemann, A. & Pfaehler, B. (1994): Growth stage-dependent effects of ozone on the permeability for ions and non-electrolytes of wheat leaves in relation to the susceptibility to Septoria nodorum Berk. Physiological and Molecular Plant Pathology 45, 153-167.

von Tiedemann, A. & Firsching, K. H. (1998): Combined whole-season effects of elevated ozone and carbon dioxide concentrations on a simulated wheat leaf rust (Puccinia recondita f. sp. tritici) epidemic. Zeitschrift Fur Pflanzenkrankheiten und Pflanzenschutz-Journal of Plant Diseases and Protection 105, 555-566.

von Tiedemann, A. & Firsching, K. H. (2000): Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. Environmental Pollution 108, 357-363.

von Tiedemann, A., Weigel, H. J. & Jaeger, H. J. (1991): Effects of open-top chamber fumigations with ozone on three fungal leaf diseases of wheat and the mycoflora of the phyllosphere. Environmental Pollution 72, 205-224.

Warwick, K. R. & Taylor, G. (1995): Contrasting effects of tropospheric ozone on five native herbs which coexist in calcareous grassland. Global Change Biology 1, 143-151.

Weber, J. A., Hogsett, W. E. & Plocher, M. D. (1997): Growth response of ponderosa pine to ozone in competition with blue wildrye. Bulletin of the Ecological Society of America 78, 328.

Wedlich, K. V., Rintoul, N., Peacock, S., Cape, J. N., Coyle, M., Toet, S., Barnes, J. & Ashmore, M. (2012): Effects of ozone on species composition in an upland grassland. Oecologia 168, 1137-1146.

Wilbourn, S., Davison, A. W. & Ollerenshaw, J. H. (1995): The use of an unenclosed field fumigation system to determine the effects of elevated ozone on a grass clover mixture. New Phytologist 129, 23-32.

Winkler, J. B., Fleischmann, F., Gayler, S., Scherb, H., Matyssek, R. & Grams, T. E. E. (2009): Do chronic aboveground O-3 exposure and belowground pathogen stress affect growth and belowground biomass partitioning of juvenile beech trees (Fagus sylvatica L.)? Plant and Soil 323, 31-44.

Woodbury, P. B., Laurence, J. A. & Hudler, G. W. (1994): Chronic ozone exposure increases the susceptibility of hybrid Populus to disease caused by Septoria musiva. Environmental Pollution 86, 109-114.

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 233, 203-211.

Zak, D. R., Holmes, W. E. & Pregitzer, K. S. (2007a): Atmospheric CO2 and O-3 alter the flow of N-15 in developing forest ecosystems. Ecology 88, 2630-2639.

Zak, D. R., Kubiske, M. E., Pregitzer, K. S. & Burton, A. J. (2012): Atmospheric CO2 and O3 alter competition for soil nitrogen in developing forests. Global Change Biology 18, 1480-1488.

Zak, D. R., Holmes, W. E., Pregitzer, K. S., King, J. S., Ellsworth, D. S. & Kubiske, M. E. (2007b): Belowground competition and the response of developing forest communities to atmospheric CO2 and O-3. Global Change Biology 13, 2230-2238.

6 Effects of ozone on ecosystem function and services

The term 'ecosystem services' is generally used to describe the benefits the society obtain from ecosystems and is one potential tool to pursue a holistic approach combining social and economic aspects (Cooter et al. 2013). Urban forests, for example, provide important ecosystem services such as carbon dioxide sequestration and removing of air pollutants (Jim & Chen 2008; Escobedo et al. 2011; Baumgardner et al. 2012; Manes et al. 2012). In general, from the view of their function ecosystems have a crucial role in regulating quality of air, soil, and water. On the other hand, ecosystems are highly vulnerable by climate change components itself and these impacts may be expressed by modifications of nutrient and carbon dynamics or hydrology.

This chapter is purposed to discuss all those phenomena and processes potentially affected by ozone, which pertain to the ecosystem as a whole and its function, respectively. The parameters considered range from primary disturbances in physiology to productivity and maintenance at the ecosystem level and also involve perturbations as being partly influenced by phytogenic volatile organic compounds. It is assumed that rising atmospheric levels of carbon dioxide (CO_2) and ozone will affect the carbon sequestration in ecosystems. While future levels of CO_2 are thought to increase C input into the soils (Lukac et al. 2009) elevated levels of ozone may alter terrestrial carbon cycling by lowering the quantity of carbon inputs into soils (Loya et al. 2003) reflecting a consequence of reduced plant productivity.

6.1 Water cycling

6.1.1 Effects on stomatal functioning

There has been long-term and wide spread evidence that elevated ozone levels alter stomatal performance and hence the stomatal conductance (g_s) of plants (Darrall 1989; Mansfield & Pearson 1996; Mansfield 1998; Robinson et al. 1998) and resulted in uncoupling of the relationship between net photosynthesis and stomatal conductance (Paoletti et al. 2007; Singh et al. 2009). Current assumptions of the possible mechanisms that may explain ozone induced stomatal closure include *i.)* reduced photosynthesis and increased sub-stomatal CO_2 concentration, *ii.)* direct impact on guard cells, *iii.)* altered calcium homeostasis, or *iv.)* altered hormone production (McAinsh et al. 2002; Paoletti & Grulke 2005; Wittig et al. 2007; Wilkinson & Davies 2010).

For **tree species** reduction in stomatal conductance for water vapour in response to ozone has been observed for several plant species e.g. *Betula pendula* (Pääkkönen et al. 1998), *Betula papyrifera* (Uddling et al. 2009), *Tilia americana* (Pellegrini et al. 2013), *Populus nigra*, *Viburnum lantana, Fraxinus excelsior* (Novak et al. 2005), *Liriodendron chinense* (Zhang et al. 2011), *Fagus crenata* (Hoshika et al. 2013b), *Quercus ilex* (Baldantoni et al. 2013), *Populus tremuloides* (Uddling et al. 2009), *Populus deltoides x Populus nigra* (Dumont et al. 2013), and *Pinus sylvestris* (Kellomaki & Wang 1997). The response was shown to be species-specific (Novak et al. 2005), clone- and exposure-dependent (Pääkkönen et al. 1998) and age-dependent (Kellomaki & Wang 1997; Wittig et al. 2007; Hoshika et al. 2013b). For birch differences between geographic areas, habitats and years seem to be existent (Kärenlampi et al. 1998). Moreover, measurements of xylem sap flow shows that the detrimental effect of ozone is dependent on weather conditions (Maiermaercker 1997).

In **grassland species** ozone was proved to decrease stomatal conductance in clover (*Trifolium pratense,* Jäggi et al. 2005; *T. repens*, Crous et al. 2006; *T. alexandrinum*, Chaudhary & Agrawal 2013), herbs (*Plantago lanceolata,* Jäggi et al. 2005; *Ranunculus acris*, Wagg et al. 2013; *Leontodon hispidus* , Mills et al. 2009; *Valeriana officinalis*, *Iris pseudacorus, Symphytum officinale, Mentha aquatica*, and *Cirsium arvense,* Power & Ashmore 2002), and grass (*Dactylis glomerata* ,Mills et al. 2009; Wagg et al. 2013). With respect to **agricultural crops** reduced stomatal conductance has been described e.g. for *Glycine max* (Jaoude et al. 2008; Singh et al. 2009), *Oryza sativa* (Sarkar & Agrawal 2012), *Solanum tuberosum* (Pleijel et al. 2002), and *Triticum aestivum* (Feng et al. 2008; Xu et al. 2009).

For soybean Jaoude et al. (2008) demonstrated that measurement of daily evapotranspiration reflect the effect of ozone on stomatal conductance which amounted up to 28 % when plants were well watered, whereas no impact was measured under water stress conditions. Calculations by means of meta-analysis revealed that effects of elevated ozone on stomatal conductance amount to a decrease by 15 % on average for trees (Novak et al. 2005; Wittig et al. 2007; Pellegrini et al. 2013) and 22 % for wheat (Feng et al. 2008). On the opposite, findings of Sun et al. (2012) supported increasing evidence that ozone at near ambient concentrations may reduce stomatal control of leaf transpiration, hence causing an increase in water use.

Long-term observations indicated that elevated ozone may cause a sluggish stomatal response i.e. a delay in stomatal responses to changing environmental conditions and this way trigger an increase in leaf water loss (McAinsh et al. 2002; Paoletti & Grulke 2010; Hoshika et al. 2012; Hoshika et al. 2013a). Thus, ozone may impair stomatal control and predispose vegetation to drought stress in forests (Paoletti 2007) and grasslands (Wagg et al. 2013). If stomata fail to close under low light or water-stressed conditions, water loss may be greater over time. In other situations, it is possible that sluggish stomata may fail to completely open in response to environmental stimuli and may result in decreased water loss. This way, elevated levels of ozone have the potential to upset the water balance of the leaf or the whole plant by affecting stomatal aperture (Robinson et al. 1998) and will amplify the adverse effects of increasing temperatures on forest growth and forest hydrology (McLaughlin et al. 2007b).

Ozone-induced physiological or growth related changes, such as reduced leaf area index and accelerated leaf senescence have also been suggested to have an effect on water-use efficiency of plants. For example, some previous and more recent chamber and field studies have shown that ozone exposure is correlated with lower foliar retention (Karnosky et al. 1996; Topa et al. 2001; Karnosky et al. 2003).

6.1.2 Effects on stand-level water balance

The role of the stomata has also been proofed at larger scales for both forests and to a lesser extent for cropland (Table 14). In a 2-year field experiment using pot-grown soybean seasonal average of daily whole-plant water loss was shown to be reduced by ozone (72 ppb) by about 28 %. As water loss per unit leaf area and water use efficiency for seed production was not significantly affected the decreased whole-plant water loss was attributed to ozone induced reduction in growth and leaf area (Booker et al. 2004). Exposure of soybean to elevated ozone (FACE) caused a decline in canopy evapotranspiration resulting in decreased water use by as much as 15 % at 1.37 times background concentrations (Bernacchi et al. 2011) and by up to 26 % at three times current ozone (VanLoocke et al. 2012).

Investigations with tree species under open air ozone exposure conditions using sap flux measurements have shown that stand-level water use per unit ground area of aspen clones was not significantly affected by elevated ozone although the treatment decreased leaf area index by 22 % and basal area by 20 % (Uddling et al. 2008). Uddling et al. (2009) attributed this result to an increase in leaf area-specific hydraulic conductance. The lack of an ozone effect on stand-level water use may also be caused by a higher proportion of sun leaves in trees under elevated ozone compared with control trees (Uddling et al. 2008).

Field studies in a deciduous forest in eastern Tennessee provided some insight into the possible consequences of stomatal sluggishness at the leaf level for ecosystem water cycling (McLaughlin et al. 2007b; McLaughlin et al. 2007a). It was found that daily ozone levels with maxima ranging from 69 to 82 ppb reduced stem growth by up to 50 % in one year with high ozone levels. The authors suggested that peak hourly ozone exposures resulted in an increase in the rate of water loss through transpiration as indicated by an increased stem sap flow. Due to the enhanced canopy water loss water uptake by the trees increased as reflected in reduced soil moisture in the rooting zone. At the landscape-level this change in tree water use was assumed to lead to further impacts on the hydrological cycle and ozone has been reported to contribute to variation in late-season streamflow by as much as 23 % in areas of highest exposure in forested watersheds in Tennessee (Sun et al. 2012). A loss in stomatal sensitivity associated with increased evapotranspiration and reduced streamflow can be expected to increase drought episodes and to have implications for flow-dependent aquatic biota (Sun et al. 2012).

Table 14: Effects of ozone on stand water use and hydrology.

ecosystem	method	effect on hydrology	reference
agro-ecosystem *Glycine max*	experimental 72 ppb	reduction of seasonal whole-plant water loss by 28 %	Booker et al. 2004
	experimental 1,3 x AA	reduction in canopy evapotranspiration by15 %	Bernacchi et al. 2011
	experimental 3 x AA	reduction in canopy evapotranspiration by 26 %	VanLoocke et al. 2012
Populus tremuloides	experimental 1,4 x AA	no effect on sap flow	Uddling et al. 2008
deciduous forests SO-USA	modelling B1§ and A2§	reduction in evapotranspiration by 4-7 % increase in streamflow by 6-7 %	Felzer et al. 2009
	modelling AA +20 ppb	reduction in water use by 3 %	Hanson et al. 2005
	modelling current ambient concentrations	increase in evapotranspiration (sap flow) reduction in streamflow by 23 %	Sun et al. 2012 McLaughlin et al. 2007a,b

§ emission scenarios (IPCC)

Recent ecosystem **models** that address the larger scale effects of ozone on water turnover are often based on the assumption that ozone induces a stomatal closure. For example, in order to assess the interactions of ozone, climate, elevated CO_2 and N limitation on the hydrological cycle in the eastern U.S., Felzer et al. (2009) used the terrestrial ecosystem model TEM-Hydro. According to this model elevated CO_2 decreased evapotranspiration by 2 % to 4 % and increased runoff by 3 % to 7 %, as compared to the effects of climate alone. Including ozone damage and N limitation into the calculations evapotranspiration was reduced by an additional 4 % to 7 % and runoff was increased by an additional 6 % to 11 %. Hanson et al. (2005) using a stand-level simulation model found a modest 3 % reduction in water use when the ozone concentration was raised by about 20 ppb above the prevailing ambient level.

6.2 Carbon cycling

6.2.1 Mechanisms of ozone-induced growth effects

Beside visible leaf injury the most commonly documented impact of elevated ozone on the single plant level exists in a reduction in productivity and has been proofed for crops, forest trees and native plants (see chapter 3). Over the past 50 years the inhibitory effect of tropospheric ozone on growth and yield was the object of investigation in numerous studies and has been reviewed frequently e.g. (Fuhrer 2002; Fiscus et al. 2005; Paoletti 2007; Gomez-Garay et al. 2013). To understand implications for the terrestrial carbon cycling it is necessary to investigate to what extent this effect could be translated to the stand and landscape level.

When interfering with elevated levels of ozone one characteristic response of all living organisms is the induction of oxidative stress. In plants, this involves an impairment of the photosynthetic apparatus, induction of detoxification processes and acceleration of senescence. Finally, each of these impairments is likely to be reflected in growth depressions to a greater or lesser extent.

It may be assumed that plant growth retardation under longer-term ozone exposure at moderately enhanced concentrations is mostly the result of reduced rates of assimilation at the leaf-level. There is clear evidence that reduction of the capability of photosynthesis is commonly observed in plants grown under elevated ozone concentrations. Reduced photosynthesis in turn may be reasoned by changes in stomatal aperture, direct cellular damage, impairment of electron transport, and/or decline in the amount and activity of Rubisco (Matyssek & Sandermann 2003; Singh et al. 2009).

Detoxification of reactive oxygen species, directly or indirectly derived from ozone exposure occurs from both existing antioxidants and those stimulated by ozone itself. Detoxification reactions require energy for regeneration of antioxidants, i.e. particularly at prolonged ozone exposure detoxification capacity may decline due to decreased rates of carbon assimilation and limited availability of energy (Wieser & Matyssek 2007). In general, cell injury or death of plant tissues occurs when the ozone uptake exceeds the detoxification capacity.

Ozone-induced physiological changes, such as reduced leaf area index and accelerated leaf senescence, have also been suggested to have an effect on stand productivity. For example, some previous and more recent chamber and field studies have shown that ozone exposure is correlated with lower foliar retention (Karnosky et al. 1996; Topa et al. 2001; Karnosky et al. 2003). From their experiments with spring wheat Pleijel et al. (1997) concluded that shortening of leaf duration by ozone may impact plant development differently, depending on the extent of the stress and may range from effects on the accumulation of total biomass only (accelerated senescence) up to influencing the carbon allocation in plants (premature senescence). Thus, along with effects on total plant productivity impaired translocation of assimilates from source (e.g. leaves) to sink organs (e.g. roots and seeds) and early senescence likely contribute to carbon and nutrient dynamic. In their meta-analysis including 125 observations Grantz et al. (2006) estimated an average reduction in the shoot:root allometric coefficient *k*, (relative ratio growth rate of the root and shoot) of 5.6 %, even though about one third of all observations yielded an increase in *k*. Wang & Taub (2010) examined root mass fraction (i.e., the fraction of root to total biomass) of mostly herbaceous species and found that, on average, ozone reduced biomass allocation by 8.5 %. Wittig et al. (2009) focused on tree species and concluded from their analysis that the root-to-shoot ratio indicated a greater sensitivity to ozone than shoot production itself. Within-tree alterations of carbon allocation due to disturbed phyto-hormonal regulation have also been shown to affect growth of mature beech trees (Winwood et al. 2007; Kitao et al. 2012). On the other hand, there are also reports on positive ozone effects on root biomass production and root-to-shoot ratios especially shown for mature trees (Pregitzer et al. 2008; Matyssek et al. 2010a; Matyssek et al. 2010b).

6.2.2 Quantification of growth reduction responses

Ecosystem-level effects have frequently been measured as either decreases in photosynthesis and increases in dark respiration, reduced biomass of total plants, or decreased rates of decomposition and reveal a general agreement among a wide range of studies in some cases (Felzer et al. 2007).

Detrimental ozone effects on growth and yield of the major global food **crop** species, such as wheat, rice, soybean and cotton have repeatedly been detected within exposure studies and yield reductions have been estimated at 24 % (70 ppb) for soybean (Morgan et al. 2003), 20 % (42 ppb) up to 60 % (153 ppb) for wheat (Feng et al. 2008), and 14 % (62 ppb) for rice (Ainsworth 2008). More recently, the only three free air ozone exposure experiments (FACE) with crops worldwide have shown that modest enhancements of ambient ozone concentrations (which ranged between 42 and 69 ppb) resulted in yield losses of 5 %-18 % for rice (Shi et al. 2009), 15 %-25 % for soybean (Morgan et al. 2006) and 10 %-35 % for wheat (Zhu et al. 2011).

According to Mills et al. (2007) more than 20 % of the European crop production area is at risk for yield losses of about 5 % at current ozone levels. Looking at East Asia, it has been estimated that in 1990 China, Japan and South Korea lost 1 % to 9 % of their yield of wheat, rice and corn and 23 % to 27 % of their yield of soybeans. Projected to the year 2020 a yield loss between 20 %-30 % is expected (Aunan et al. 2000; Wang & Mauzerall 2004).

Assessments of present day **global relative yield** indicate that yield reductions range from 5.3 % for potato up to 19.0 % for bean (Feng & Kobayashi 2009) and losses may vary in the range of 8.5 % and 16 % for soybean, 3.9 % and 15 % for wheat, 2.2 % and 5.5 % for maize and 3 % and 4 % for rice depending on exposure index used (Van Dingenen et al. 2009; Avnery et al. 2011).

Overall, the above examples all provide reasonable evidence that the productivity of important agro-ecosystems are at risk from current and future ozone exposure. From the perspective of the growing global population with ever increasing future needs for food supply, the estimated yield losses of these crops are of concern.

Forest productivity is of particular interest not only for timber production but also due to its implications for the global carbon cycle and climate change as forest soils account for a large part of the stable carbon pool held in terrestrial ecosystems (Lukac et al. 2009). Current ozone levels are considered an important stressor of over 30 % of the world's forests (IPCC 2007; Royal Society 2008) and also constitute a risk for forests in Europe (Ashmore 2005; Matyssek et al. 2008).

Because of the difficulties in scaling ozone effects from seedlings to mature forest trees, calculations for forest productivity are limited. Wittig et al. (2009), for example, analysed growth responses of tree species representative of northern hemisphere forests from 263 studies over the past 40 years and found that elevated ozone concentrations (97 ppb) decreased annual total biomass growth by 11 % to 17 %. A simulation of forest growth at a Swedish site predicted that prevailing mean ozone exposure during 1993-2003 had the potential to reduce forest growth by 2.2 % (Karlsson et al. 2005). Recently, for Switzerland growth loss by ozone exposure of forest trees has been estimated to amount to 19.5 % for deciduous forests and 6.6 % for coniferous forests based on annual ozone stomatal uptake during the time period 1991-2011 (Braun et al. 2014).

Grasslands comprise a variety of habitats described as meadows and fens, as well as agricultural grassland used for grazing. Although there is some evidence of growth effects on single grassland species or artificial mixtures estimating the response of grassland communities to ozone in terms of their productivity is difficult because of their multispecies character and the various kinds of interaction. Studies on grassland communities of high conservation value have shown that their net primary production is quite resilient to elevated ozone (Bassin et al. 2007; Volk et al. 2011). However, studies on this ecosystem more often focussed on other endpoints than total productivity such as species composition. Recently, results of an ozone exposure study (OTC) on an annual pasture in Spain showed a reduction of total yield by 21 % (Calvete-Sogo et al. 2014). A significant reduction in gross primary production (GPP) by elevated ozone resulted from both, a global reduction of ecosystem assimilation and an increase of ecosystem respiration.

6.2.3 Scaling up to landscape-level

Ozone effects on plant vigour, water relations and soil processes may finally all contribute to altered net primary productivity and carbon sequestration which is one of the key features of ecosystem function. For example, a recent analysis of results from different experimental ozone fumigation studies with tree species covering ambient or near-ambient concentrations revealed that ozone levels of approximately 40 ppb can suppress net assimilation rate on average by 11 % (Wittig et al. 2007). Summarising 53 ozone exposure studies with soybean in a meta-analytic approach Morgan et al. (2003) found a ~20 % reduction in net assimilation rate due to an average ozone exposure of 70 ppb.

Within the past 10 years research activities on ozone response issues comprised increasingly estimations on large-scale balance of primary productivity and carbon exchange by means of both, experimental and modelling efforts.

Various simulations of the potential effects of historical or current ozone exposures by means of modelling have been performed at the landscape or country-level (Table 15), for example by incorporating empirical equations derived for trees and crops into the Terrestrial Ecosystem Model (Felzer et al. 2004) or by combining leaf-level ozone response data from ozone fumigation studies with a Forest Ecosystem Model (Ollinger et al. 1997). Translating yield reduction into total biomass loss Pleijel et al. (2014) estimated above-ground biomass losses due to ozone in 2000 in Europe of about 22.2 Tg (million tonnes).

Table 15: Modelling impacts of ozone on primary production and carbon storage in response to historical ozone levels.

site/ecosystem/time	reduction in primary production	reduction in carbon storage	reference
Vegetation in the Mediterranean Basin in 2002	22 % (GPP)		Anav et al. 2011; 2012
China's terrestrial ecosystems from 1961 to 2000	4.5 % (NPP)	0.2-6.9 %	Ren et al. (2007)
China's forest ecosystems from 1961 to 2005		7.7 %	Ren et al. (2011)
the United States 1980s to early 1990s	2.6 % - 6.8 % (NPP)		Felzer et al. (2004)
the United States 1980s to early 1990s	3 % - 5 % (NPP)	5 % - 23% 24 - 68 Tg C yr^{-1}	Felzer et al. (2002)
the United States since 1950s		18 - 38 Tg C yr^{-1}	Felzer et al. (2004)
64 locations Northeastern United States 1987 to 1992	3 % - 16 % (NPP)		Ollinger et al. (1997)

(NPP =net primary production or GPP =gross primary production)

All model simulations given in Table 15 resulted in a considerable reduction in **net primary productivity (NPP)**, independently from the ecosystem and country site considered. In contrast, calculations based on experimental approaches evidenced a more conservative valuation. De Marco et al. (2013) applied a Generalised Linear/non-Linear regression model to assess cause-effect relationships between primary productivity of *Quercus cerris*, *Quercus ilex* and *Fagus sylvatica* and climate and pollutants including ozone in Italy and concluded that ozone did not significantly affect net primary productivity. In the course of the Aspen FACE study a decrease in leaf mass by 13 % and a reduction in NPP by 10 % due to elevated ozone was detected, but this effect gradually disappeared during the final seven years of the experiment (Talhelm et al. 2012; Talhelm et al. 2014). Thus, the authors concluded that the effect on NPP will be smaller than expected. Similarly, Landry et al. (2013) described a spatial pattern of impacts for Canadian forests and concluded that at the landscape-level the impacts of ozone are likely below detection.

Changes in **soil C content** have been investigated within the framework of FACE studies. After four years of fumigation less carbon entered the soil of mixed aspen forest due to the exposure to elevated ozone when CO_2 was simultaneously enhanced (Loya et al. 2003). After 11 years of exposure the effect of elevated ozone on soil carbon content ranged from none (0.2 m depth) to a decrease by 9 % in the top 0.1 m (Talhelm et al. 2009; Talhelm et al. 2014). Hofmockel et al. (2011) calculated the ozone-induced reduction of total soil carbon formation to amount approximately 300 g C m^{-2} compared to the amount formed under elevated CO_2 alone. Within a Chinese crop FACE (rice/wheat rotation) elevated ozone decreased the soil organic C concentration by 17 % and 5.6 %, respectively, depending on depth layers (Kou et al. 2014).

6.3 Flowering and reproduction

Studies during recent decades have demonstrated that various stages of reproductive development are clearly sensitive to ozone. An overview on the impact of ozone on plant reproduction can be found at Black et al. (2000), including the effects on yield of seed crops. They concluded that negative effects on the reproductive performance in response to ozone may result from a reduction in plant growth, a decreased reproductive allocation, or from direct effects on reproductive structures.

A recent meta-analysis of ozone effects on plant reproductive growth and development indicated that ozone at current ambient concentrations significantly reduced seed number, fruit number and fruit weight, while there was a trend towards increasing flower number and flower weight at elevated ozone (Leisner & Ainsworth 2012). Exposure to elevated ozone reduced the flower or seed biomass in three therophytic clover species, *Trifolium cherleri, T. subterraneum*, and *T. striatum* (Gimeno et al. 2004). For *Rubus cuneifolius* exposure to ozone resulted in an initial acceleration in flowering while the total number of fruits was not significantly different among treatments (Chappelka 2002). Plants of *Apocynum androsaemifolium* grown in ambient air produced significantly less flowers and fruits than those grown in the absence of ozone, moreover, surviving rate to mature fruits was significant lower, when flowers had been produced in ambient air (Bergweiler & Manning 1999).

Bender et al. (2006) observed contrasting effects on resource allocation to the vegetative and reproductive organs of 17 herbaceous species that were exposed to different ozone regimes from the seedling stage until seed maturation. Although exposure caused comparable reductions in both vegetative and reproductive growth in the majority of the investigated species, three species (*Chenopodium album, Matricaria discoidea,* and *Stellaria media*) showed reduced reproductive allocation while vegetative growth was stimulated. On the other hand plants of the crop species *Brassica napus* tended to develop longer raceme branches, indicating a possible compensation response for an initial ozone-induced bud abortion (Bosac et al. 1994), similar to a mechanism which has been interpreted as a compensatory reproductive responses by Black et al. (2010).

Germinability of the seeds coming from ozone exposed plants was affected by ozone such that germination rate was up to 30 % lower in ozone-treated plants compared to control plants (*Chenopodium album, Papaver rhoeas*, and *Urtica urens*, Bender et al. 2006). Similarly, at the Aspen FACE site the effects of elevated ozone on reproductive fitness in paper birch (*Betula papyrifera*) was investigated indicating that ozone significantly increased flowering, but decreased seed weight and germination rate, thus, the reproductive fitness of this species was affected (Darbah et al. 2007; Darbah et al. 2008). By contrast, seeds of *Brassica campestris* germinated more rapidly when plants had been exposed to ozone, irrespective of the stage of floral development during exposure (Black et al. 2012).

Within a weed community exposed to ozone during four years phenotypic changes *Spergula arvensis* populations has been shown by changes in seed traits as germination, dormancy and longevity, which may have implications for the persistence of the weed in the field and for weed-crop interactions (Landesmann et al. 2013).

There is some research activity focussing on pollen quality and vitality. A single exposure of pollen of *Brassica napus* to ozone had no significant effect on either pollen germination or pollen tube growth (Bosac et al. 1993), whereas exposure to ozone was found to cause a disrupted development of pollen in *Lolium perenne* (Schoene et al. 2004) and a reduction in pollen germinability of *Pinus sylvestris* (Abraitiene et al. 2002). These results suggest that ozone can significantly affect resource allocation patterns and reproductive fitness which may have significant implications for the establishment, performance, and survival of the progeny and hence for productivity, structure and function of the community.

Any impact of ozone exposure on the timing of flowering may also play an important role in reproductive success, particularly for species in which flowering is closely synchronized with pollinating species (Black et al. 2000; Hayes et al. 2012). However, the impact of ozone on the timing of flowering varies markedly between species. For example, ozone exposure has been reported to delay flowering in two species (*Campanula rotundifolia* and *Vicia cracca*) of simulated meadow community mesocosms (Rämö et al. 2007). In mesocosms representing 'calcareous grassland', ozone has been found to accelerate the timing of the maximum number of flowers in *Lotus corniculatus* (Hayes et al. 2012). By contrast, Bergmann et al. (1996) showed that the timing of flowering and seed set in 17 wild plant species were not significantly influenced by season-long exposure to 1.5 x ambient ozone concentration in OTCs.

6.4 Floral volatile organic compounds

Volatile hydrocarbons (VOCs) emitted from the vegetation contribute to the formation of tropospheric ozone but in turn elevated concentrations of ozone may affect VOC emission from plants. Thus, phytogenic VOCs interact significantly with climate change parameters, although the underlying effects on the biochemical reactions and physiological conditions are still uncertain (Calfapietra et al. 2013). Furthermore, phytogenic VOCs play an important role in plant-insect interactions and adaptation to stress, as some substances are known to be emitted by plants in response to herbivore attack. In recent years, the involvement of ozone into these various interactions has gained more attention and has been reviewed several times (Calfapietra et al. 2009; Iriti & Faoro 2009; Yuan et al. 2009; Pinto et al. 2010; Calfapietra et al. 2013).

6.4.1 VOCs emission and climate change

Isoprene is the most abundant VOC emitted by plants and species of the genera *Quercus* and *Populus* are known to be strong emitters (http://www.2020-horizon.com/GLOBALVOC-Understanding-global-change-effects-on-VOC-emission-in-Populus-from-eco-physiological-to-molecular-level%28GLOBALVOC%29-s25782.html). In this context, a discussion arose concerning efforts to select urban tree species according to a low VOCs emission potential. Italian vegetation, for example, includes several species that are strong and evergreen isoprenoid emitters (Calfapietra et al. 2009). Moreover, VOC emission rate is significantly related to temperature (Hartikainen et al. 2012). However, it has been argued that some progress in land use practise may be counter-productive. Some of the plant species cultivated as bioenergy crops emit more isoprene than the traditional crops (Ashworth et al. 2013).

Independently from their causing agent adverse physiological changes such as effects on the photosynthetic capacity may result in a decrease in precursors needed for the biosynthesis of VOCs (Pinto et al. 2010). On the other hand, biosynthesis of VOCs represents one mechanism in coping with abiotic stress (e.g. high temperatures and oxidative stress) and plays an important role in the ozone-induced detoxification cascade.

When occurring at elevated levels tropospheric ozone by itself has the potential to change the volatile emission profile from plants. Under controlled environment long-term exposure to ozone (50 ppb) caused a 40 % increased emissions of monoterpenes in *Pinus sylvestris* (Heiden et al. 1999). Averaged on four evergreen trees representative of natural Mediterranean vegetation Llusia et al. (2002) estimated an increase in total VOC emission rates by 45 %, when exposed to ozone in OTCs (NF+40 ppb). As shown in free air exposure experiments emission of terpenoids from *Picea abies* was doubled, when daytime ozone concentrations exceeded 40 ppb (Kivimaenpaa et al. 2013). Similar responses to ozone have been reported for tomato (Penuelas et al. 1999; Mina et al. 2010). However, the response to ozone of different plant species is found to be very variable, depending on genetic and environmental factors. Experiments on *Populus* clones showed that the emission of VOC in response to ozone may vary depending on genotypic differences as either monoterpenes or sesquiterpenes increased under elevated ozone, while, quantities of non-terpene hydrocarbon emission from both clones significantly decreased (Pellegrini et al. 2012). Isoprene emission from two aspen clones (*Populus tremuloides*) decreased significantly under elevated ozone in the sensitive clone, but only slightly in the tolerant clone (Blande et al. 2007). Calfapietra et al. (2008) concluded that ozone tolerance in poplar is related to the capacity to maintain higher amounts of isoprene emission.

There are also reports indicating a reduction in terpene emission for example for *Betula pendula* when exposed under free air (Hartikainen et al. 2012), or for herbaceous plants as *Brassica napus* (Himanen et al. 2009) or two leguminous species representative for Mediterranean pastures, *Ornithopus compressus* and *Trifolium striatum* (Llusia et al. 2014). Similarly, methane emissions from peatland was shown to be reduced by about 25 %, in response to elevated ozone (49 ppb) during midsummer period (Toet et al. 2011). On the other hand, emissions of monoterpenes from *Picea abies* (Lindskog & Potter 1995), emissions of total VOCs from *Pinus halepensis* (Penuelas et al. 1999), and *Betula pendula* remained unaffected (Vuorinen et al. 2005) after exposure within OTCs. Studying the isoprene emission of a boreal Sphagnum fen under long-term realistically elevated ozone concentration in open-field conditions Tiiva et al. (2007) found no effect on isoprene emission, although there was a slight increase during the warmest weather conditions.

6.4.2 Signaling

Floral volatile hydrocarbons play also an important role in plant-plant communication and plant-animal interactions over short distances and are involved in the attraction of pollinators, herbivores, and their natural enemies (Iriti & Faoro 2009; Blande et al. 2010; Pinto et al. 2010). When emitted from plants to the atmosphere VOCs are susceptible to direct chemical reactions with oxidants as ozone (Pinto et al. 2007b; Pinto et al. 2007a; McFrederick et al. 2008; Fuentes et al. 2013), and as a result, these chemical signals were potentially degraded and lose their specificity (Pinto et al. 2007a; McFrederick et al. 2009).

Acalymma vittatum, a cucumber beetle, for example, uses floral VOCs to locate its host plant *Cucurbita foetidissima*. The study of Fuentes et al. (2013) clearly showed, that the beetles chose their host flower less frequently, when ozone levels increased above 80 ppb. Ozone exposure experiments with a tritrophic system have been performed in order to investigate the orientation behaviour of a natural enemy of herbivores (e.g. predatory mites) that are known to detect VOCs emitted by the herbivore-infested plants (e.g. *Phaseolus lunatus* or *Brassica oleracea*) to locate their prey. The results indicated that predators or parasitoids were equally attracted to ozone-exposed and unexposed plants (Vuorinen et al. 2004; Pinto et al. 2007b).

McFrederick et al. (2008) assumed that increased air pollution interferes also with pollinator attracting hydrocarbon signals. Pollinators that rely on scents to orient to flowers are likely to spend more time for searching for forage, which could affect their reproductive fitness, but could also affect plant reproduction as reduced pollinator efficiency could result in greater pollinator limitation (McFrederick et al. 2008). The implications of the loss or modification of scent signals by ozone pollution may be exacerbated in patchy or fragmented landscapes having large ecological impacts in terms of reproduction success of vegetation and food supply of nectar feeding insects.

6.5 Conclusion

When transferring experimental exposure response data of single plants or model communities to the ecosystem or landscapes level there are numerous factors to be taken into account: Species composition of ecosystems, stand development processes, exposure dynamics, and seasonal differences play an important role. In this context, cumulative NPP has been proved to be a strong predictor of ecosystem carbon content.

Recent findings indicate that rising levels of ozone may have potential impacts on terrestrial carbon sinks and regional hydrology by reducing the capability of vegetation to assimilate carbon and altering transfer of water vapour into the atmosphere. In consequence, soil carbon formation rates were lowered and more carbon dioxide accumulates in the atmosphere, especially under elevated CO_2. Therefore, it is suggested that global-scale reductions of productivity of terrestrial ecosystems (mainly forests) indirectly contribute to climate change and global warming and simultaneously the capacity of forests to mitigate global climate change will be impaired (Loya et al. 2003; Felzer et al. 2005; Sitch et al. 2007; Sun et al. 2012).

To enhance our understanding of how elevated levels of ozone impact the ecosystems function further investigation are proposed to address multifactor experiments in the field (Ren & Tian 2007) and changes in soil carbon (Talhelm et al. 2009; Talhelm et al. 2014), for example.

Since VOCs are precursors of ozone, an increased VOC emission as a consequence of elevated ozone concentrations in the troposphere may lead to feedback mechanisms in photo-oxidant formation. It has been shown that elevated levels of ozone interfere with phytogenic VOCs in different ways. In general, ozone-induced changes in flowering timing and signaling could have large ecological impacts, affecting plant pollination, the food supply of nectar feeding insects or defence against herbivory. Therefore, recent findings highlight the importance of eco-physiological parameters being taken into account into future research on ecosystem level effects of ozone.

Beside these indirect effects on pollination, ozone is supposed to affect pollen vitality directly during flowering and this way, changes in the genetic structure in the next generation are possible (Abraitiene et al. 2002).

6.6 References

Abraitiene, A., Kairiukstis, L., Pliura, A., Girgzdiene, R. & Abraitis, R. (2002): Variation in germination of Scots pine (Pinus sylvestris L.) pollen exposed to ozone. Baltic Forestry 8, 2-7.

Ainsworth, E. A. (2008): Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration. Global Change Biology 14, 1642-1650.

Anav, A., Menut, L., Khvorostyanov, D. & Viovy, N. (2011): Impact of tropospheric ozone on the Euro-Mediterranean vegetation. Global Change Biology 17, 2342-2359.

Anav, A., Menut, L., Khvorostyanov, D. & Viovy, N. (2012): A comparison of two canopy conductance parameterizations to quantify the interactions between surface ozone and vegetation over Europe. Journal of Geophysical Research-Biogeosciences 117 (G3) DOI: 10.1029/2012JG001976.

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

Ashworth, K., Wild, O. & Hewitt, C. N. (2013): Impacts of biofuel cultivation on mortality and crop yields. Nature Climate Change 3, 492-496.

Aunan, K., Berntsen, T. K. & Seip, H. M. (2000): Surface ozone in China and its possible impact on agricultural crop yields. Ambio 29, 294-301.

Avnery, S., Mauzerall, D. L., Liu, J. F. & Horowitz, L. W. (2011): Global crop yield reductions due to surface ozone exposure: 1. Year 2000 crop production losses and economic damage. Atmospheric Environment 45, 2284-2296.

Baldantoni, D., Bellino, A., Manes, F. & Alfani, A. (2013): Ozone fumigation of Quercus ilex L. slows down leaf litter decomposition with no detectable change in leaf composition. Annals of Forest Science 70, 571-578.

Bassin, S., Volk, M., Suter, M., Buchmann, N. & Fuhrer, J. (2007): Nitrogen deposition but not ozone affects productivity and community composition of subalpine grassland after 3 yr of treatment. New Phytologist 175, 523-534.

Baumgardner, D., Varela, S., Escobedo, F. J., Chacalo, A. & Ochoa, C. (2012): The role of a peri-urban forest on air quality improvement in the Mexico City megalopolis. Environmental Pollution 163, 174-183.

Bender, J., Bergmann, E. & Weigel, H. J. (2006): Responses of biomass production and reproductive development to ozone exposure differ between european wild plant species. Water Air and Soil Pollution 176, 253-267.

Bergmann, E., Bender, J. & Weigel, H. J. (1996): Effects of Chronic Ozone Stress on Growth and Reproduction Capacity of Native Herbaceous Plants. In: Exceedance of Critical Loads and Levels - Spatial and Temporal Interpretation of Elements in Landscape Sensitivity to Atmospheric Pollutants (ed. by M. Knopflacher, J. Schneider &G. Soja), Umweltbundesamt Österreich, Wien, pp. 177-185.

Bergweiler, C. J. & Manning, W. J. (1999): Inhibition of flowering and reproductive success in spreading dogbane (Apocynum androsaemifolium) by exposure to ambient ozone. Environmental Pollution 105, 333-339.

Bernacchi, C. J., Leakey, A. D. B., Kimball, B. A. & Ort, D. R. (2011): Growth of soybean at future tropospheric ozone concentrations decreases canopy evapotranspiration and soil water depletion. Environmental Pollution 159, 1464-1472.

Black, V. J., Black, C. R., Roberts, J. A. & Stewart, C. A. (2000): Impact of ozone on the reproductive development of plants. New Phytologist 147, 421-447.

Black, V. J., Stewart, C. A., Roberts, J. A. & Black, C. R. (2010): Direct effects of ozone on reproductive development in Plantago major L. populations differing in sensitivity. Environmental and Experimental Botany 69, 121-128.

Black, V. J., Stewart, C. A., Roberts, J. A. & Black, C. R. (2012): Timing of exposure to ozone affects reproductive sensitivity and compensatory ability in Brassica campestris. Environmental and Experimental Botany 75, 225-234.

Blande, J. D., Holopainen, J. K. & Li, T. (2010): Air pollution impedes plant-to-plant communication by volatiles. Ecology Letters 13, 1172-1181.

Blande, J. D., Tiiva, P., Oksanen, E. & Holopainen, J. K. (2007): Emission of herbivore-induced volatile terpenoids from two hybrid aspen (Populus tremula x tremuloides) clones under ambient and elevated ozone concentrations in the field. Global Change Biology 13, 2538-2550.

Booker, F. L., Fiscus, E. L. & Miller, J. E. (2004): Combined effects of elevated atmospheric carbon dioxide and ozone on soybean whole-plant water use. Environmental Management 33, S355-S362.

Bosac, C., Roberts, J. A., Black, V. J. & Black, C. R. (1994): Impact of O3 and SO2 on reproductive development in oilseed rape (Brassica napus L) .2. Reproductive site losses. New Phytologist 126, 71-79.

Bosac, C., Black, V. J., Black, C. R., Roberts, J. A. & Lockwood, F. (1993): Impact of O3 and SO2 on reproductive development in oilseed rape (Brassica napus L) .1. Pollen germination and pollen tube growth. New Phytologist 124, 439-446.

Braun, S., Schindler, C. & Rihm, B. (2014): Growth losses in Swiss forests caused by ozone: Epidemiological data analysis of stem increment of Fagus sylvatica L. and Picea abies Karst. Environmental Pollution 192, 129-138.

Calfapietra, C., Fares, S. & Lofeto, F. (2009): Volatile organic compounds from Italian vegetation and their interaction with ozone. Environmental Pollution 157, 1478-1486.

Calfapietra, C., Mugnozza, G. S., Karnosky, D. F., Loreto, F. & Sharkey, T. D. (2008): Isoprene emission rates under elevated CO(2) and O(3) in two field-grown aspen clones differing in their sensitivity to O(3). New Phytologist 179, 55-61.

Calfapietra, C., Fares, S., Manes, F., Morani, A., Sgrigna, G. & Loreto, F. (2013): Role of Biogenic Volatile Organic Compounds (BVOC) emitted by urban trees on ozone concentration in cities: A review. Environmental Pollution 183, 71-80.

Calvete-Sogo, H., Elvira, S., Sanz, J., Gonzalez-Fernandez, I., Garcia-Gomez, H., Sanchez-Martin, L., Alonso, R. & Bermejo-Bermejo, V. (2014): Current ozone levels threaten gross primary production and yield of Mediterranean annual pastures and nitrogen modulates the response. Atmospheric Environment 95, 197-206.

Chappelka, A. H. (2002): Reproductive development of blackberry (Rubus cuneifolius), as influenced by ozone. New Phytologist 155, 249-255.

Chaudhary, N. & Agrawal, S. B. (2013): Intraspecific responses of six Indian clover cultivars under ambient and elevated levels of ozone. Environmental Science and Pollution Research 20, 5318-5329.

Cooter, E. J., Rea, A., Bruins, R., Schwede, D. & Dennis, R. L. (2013): The role of the atmosphere in the provision of ecosystem services. Science of the Total Environment 448, 197-208.

Crous, K. Y., Vandermeiren, K. & Ceulemans, R. (2006): Physiological responses to cumulative ozone uptake in two white clover (Trifolium repens L. cv. Regal) clones with different ozone sensitivity. Environmental and Experimental Botany 58, 169-179.

Darbah, J. N. T., Kubiske, M. E., Nelson, N., Oksanen, E., Vaapavuori, E. & Karnosky, D. F. (2007): Impacts of elevated atmospheric CO2 and O-3 on paper birch (Betula papyrifera): Reproductive fitness. Thescientificworldjournal 7, 240-246.

Darbah, J. N. T., Kubiske, M. E., Nelson, N., Oksanen, E., Vapaavuori, E. & Karnosky, D. F. (2008): Effects of decadal exposure to interacting elevated CO 2 and/or O 3 on paper birch (Betula papyrifera) reproduction. Environmental Pollution 155, 446-452.

Darrall, N. M. (1989): The effect of air-pollutants on physiological processes in plants. Plant Cell and Environment 12, 1-30.

De Marco, A., Screpanti, A., Attorre, F., Proietti, C. & Vitale, M. (2013): Assessing ozone and nitrogen impact on net primary productivity with a Generalised non-Linear Model. Environmental Pollution 172, 250-263.

Dumont, J., Spicher, F., Montpied, P., Dizengremel, P., Jolivet, Y. & Le Thiec, D. (2013): Effects of ozone on stomatal responses to environmental parameters (blue light, red light, CO2 and vapour pressure deficit) in three Populus deltoides x Populus nigra genotypes. Environmental Pollution 173, 85-96.

Escobedo, F. J., Kroeger, T. & Wagner, J. E. (2011): Urban forests and pollution mitigation: Analyzing ecosystem services and disservices. Environmental Pollution 159, 2078-2087.

Felzer, B., Kicklighter, D. W., Melillo, J. M., Wang, C., Zhuang, Q. & Prinn, R. (2002): Ozone effects on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. Report No. 9, Joint Program on the Science and Policy of Global Change, Cambridge MA, 27pp.

Felzer, B., Kicklighter, D., Melillo, J., Wang, C., Zhuang, Q. & Prinn, R. (2004): Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. Tellus Series B-Chemical and Physical Meteorology 56, 230-248.

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., Melilloa, J. M. & Wang, X. D. (2007): Impacts of ozone on trees and crops. Comptes Rendus Geoscience 339, 784-798.

Felzer, B. S., Cronin, T. W., Melillo, J. M., Kicklighter, D. W. & Schlosser, C. A. (2009): Importance of carbon-nitrogen interactions and ozone on ecosystem hydrology during the 21st century. Journal of Geophysical Research-Biogeosciences 114, DOI: 10.1029/2009jg001083.

Feng, Z. Z. & Kobayashi, K. (2009): Assessing the impacts of current and future concentrations of surface ozone on crop yield with meta-analysis. Atmospheric Environment 43, 1510-1519.

Feng, Z. Z., Kobayashi, K. & Ainsworth, E. A. (2008): Impact of elevated ozone concentration on growth, physiology, and yield of wheat (Triticum aestivum L.): a meta-analysis. Global Change Biology 14, 2696-2708.

Fiscus, E. L., Booker, F. L. & Burkey, K. O. (2005): Crop responses to ozone: uptake, modes of action, carbon assimilation and partitioning. Plant Cell and Environment 28, 997-1011.

Fuentes, J. D., Roulston, T. H. & Zenker, J. (2013): Ozone impedes the ability of a herbivore to find its host. Environmental Research Letters 8, DOI: 10.1088/1748-9326/8/1/014048.

Fuhrer, J. (2002): Ozone impacts on vegetation. Ozone-Science & Engineering 24, 69-74.

Gimeno, B. S., Bermejo, V., Sanz, J., De la Torre, D. & Gil, J. M. (2004): Assessment of the effects of ozone exposure and plant competition on the reproductive ability of three therophytic clover species from Iberian pastures. Atmospheric Environment 38, 2295-2303.

Gomez-Garay, A., Calderon Guerrero, C., Saiz de Omenaca, J. A. & Manzanera, J. A. (2013): Ozone effects on forests. African Journal of Biotechnology 12, 320-326.

Grantz, D. A., Gunn, S. & Vu, H. B. (2006): O-3 impacts on plant development: a meta-analysis of root/shoot allocation and growth. Plant Cell and Environment 29, 1193-1209.

Hanson, P. J., Wullschleger, S. D., Norby, R. J., Tschaplinski, T. J. & Gunderson, C. A. (2005): Importance of changing CO2, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. Global Change Biology 11, 1402-1423.

Hartikainen, K., Riikonen, J., Nerg, A. M., Kivimaenpaa, M., Ahonen, V., Tervahauta, A., Karenlampi, S., Maenpaa, M., Rousi, M., Kontunen-Soppela, S., Oksanen, E. & Holopainen, T. (2012): Impact of elevated temperature and ozone on the emission of volatile organic compounds and gas exchange of silver birch (Betula pendula Roth). Environmental and Experimental Botany 84, 33-43.

Hayes, F., Williamson, J. & Mills, G. (2012): Ozone pollution affects flower numbers and timing in a simulated BAP priority calcareous grassland community. Environmental Pollution 163, 40-47.

Heiden, A. C., Hoffmann, T., Kahl, J., Kley, D., Klockow, D., Langebartels, C., Mehlhorn, H., Sandermann, H., Schraudner, M., Schuh, G. & Wildt, J. (1999): Emission of volatile organic compounds from ozone-exposed plants. Ecological Applications 9, 1160-1167.

Himanen, S. J., Nerg, A.-M., Nissinen, A., Pinto, D. M., Stewart, C. N., Jr., Poppy, G. M. & Holopainen, J. K. (2009): Effects of elevated carbon dioxide and ozone on volatile terpenoid emissions and multitrophic communication of transgenic insecticidal oilseed rape (Brassica napus). New Phytologist 181, 174-186.

Hofmockel, K. S., Zak, D. R., Moran, K. K. & Jastrow, J. D. (2011): Changes in forest soil organic matter pools after a decade of elevated CO2 and O-3. Soil Biology & Biochemistry 43, 1518-1527.

Hoshika, Y., Omasa, K. & Paoletti, E. (2013a): Both ozone exposure and soil water stress are able to induce stomatal sluggishness. Environmental and Experimental Botany 88, 19-23.

Hoshika, Y., Watanabe, M., Inada, N. & Koike, T. (2012): Ozone-induced stomatal sluggishness develops progressively in Siebold's beech (Fagus crenata). Environmental Pollution 166, 152-156.

Hoshika, Y., Watanabe, M., Inada, N. & Koike, T. (2013b): Model-based analysis of avoidance of ozone stress by stomatal closure in Siebolds beech (Fagus crenata). Annals of Botany 112, 1149-1158.

IPCC (2007): Climate Change 2007: Synthesis Report Contribution of working groups I, II and II to the fourth assessment report of the IPCC. IPCC, Geneva.

Iriti, M. & Faoro, F. (2009): Chemical Diversity and Defence Metabolism: How Plants Cope with Pathogens and Ozone Pollution. International Journal of Molecular Sciences 10, 3371-3399.

Jäggi, M., Saurer, M., Volk, M. & Fuhrer, J. (2005): Effects of elevated ozone on leaf delta C-13 and leaf conductance of plant species grown in semi-natural grassland with or without irrigation. Environmental Pollution 134, 209-216.

Jaoude, M. B., Katerji, N., Mastrorilli, M. & Rana, G. (2008): Analysis of the effect of ozone on soybean in the Mediterranean region I. The consequences on crop-water status. European Journal of Agronomy 28, 508-518.

Jim, C. Y. & Chen, W. Y. (2008): Assessing the ecosystem service of air pollutant removal by urban trees in Guangzhou (China). Journal of Environmental Management 88, 665-676.

Kärenlampi, L., Metsarinne, S. & Pääkkönen, E. (1998): Stomatal conductance of birch leaves - Plenty of variation in the variable which determines the ozone dose. Chemosphere 36, 675-678.

Karlsson, P. E., Pleijel, H., Belhaj, M., Danielsson, H., Dahlin, B., Andersson, M., Hansson, M., Munthe, J. & Grennfelt, P. (2005): Economic assessment of the negative impacts of ozone on crop yields and forest production. A case study of the estate Ostads Sateri in southwestern Sweden. Ambio 34, 32-40.

Karnosky, D. F., Gagnon, Z. E., Dickson, R. E., Coleman, M. D., Lee, E. H. & Isebrands, J. G. (1996): Changes in growth, leaf abscission, and biomass associated with seasonal tropospheric ozone exposures of Populus tremuloides clones and seedlings. Canadian Journal of Forest Research 26, 23-37.

Karnosky, D. F., Zak, D. R., Pregitzer, K. S., Awmack, C. S., Bockheim, J. G., Dickson, R. E., Hendrey, G. R., Host, G. E., King, J. S., Kopper, B. J., Kruger, E. L., Kubiske, M. E., Lindroth, R. L., Mattson, W. J., McDonald, E. P., Noormets, A., Oksanen, E., Parsons, W. F. J., Percy, K. E., Podila, G. K., Riemenschneider, D. E., Sharma, P., Thakur, R., Sober, A., Sober, J., Jones, W. S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W. & Isebrands, J. G. (2003): Tropospheric O-3 moderates responses of temperate hardwood forests to elevated CO2: a synthesis of molecular to ecosystem results from the Aspen FACE project. Functional Ecology 17, 289-304.

Kellomaki, S. & Wang, K. Y. (1997): Effects of elevated O-3 and CO2 concentrations on photosynthesis and stomatal conductance in Scots pine. Plant Cell and Environment 20, 995-1006.

Kitao, M., Winkler, J. B., Low, M., Nunn, A. J., Kuptz, D., Haberle, K. H., Reiter, I. M. & Matyssek, R. (2012): How closely does stem growth of adult beech (Fagus sylvatica) relate to net carbon gain under experimentally enhanced ozone stress? Environmental Pollution 166, 108-115.

Kivimaenpaa, M., Riikonen, J., Ahonen, V., Tervahauta, A. & Holopainen, T. (2013): Sensitivity of Norway spruce physiology and terpenoid emission dynamics to elevated ozone and elevated temperature under open-field exposure. Environmental and Experimental Botany 90, 32-42.

Kou, T. J., Wang, L. R., Zhu, J. G., Xie, Z. B. & Wang, Y. L. (2014): Ozone pollution influences soil carbon and nitrogen sequestration and aggregate composition in paddy soils. Plant and Soil 380, 305-313.

Landesmann, J. B., Gundel, P. E., Martinez-Ghersa, M. A. & Ghersa, C. M. (2013): Ozone Exposure of a Weed Community Produces Adaptive Changes in Seed Populations of Spergula arvensis. Plos One 8, DOI: 10.1371/journal.pone.0075820.

Landry, J. S., Neilson, E. T., Kurz, W. A. & Percy, K. E. (2013): The impact of tropospheric ozone on landscape-level merchantable biomass and ecosystem carbon in Canadian forests. European Journal of Forest Research 132, 71-81.

Leisner, C. P. & Ainsworth, E. A. (2012): Quantifying the effects of ozone on plant reproductive growth and development. Global Change Biology 18, 606-616.

Lindskog, A. & Potter, A. (1995): Terpene emission and ozone stress. Chemosphere 30, 1171-1181.

Llusia, J., Penuelas, J. & Gimeno, B. S. (2002): Seasonal and species-specific response of VOC emissions by Mediterranean woody plant to elevated ozone concentrations. Atmospheric Environment 36, 3931-3938.

Llusia, J., Bermejo-Bermejo, V., Calvete-Sogo, H. & Peñuelas, J. (2014): Decreased rates of terpene emissions in Ornithopus compressus L. and Trifolium striatum L. by ozone exposure and nitrogen fertilization. Environmental Pollution 194, 69-77.

Loya, W. M., Pregitzer, K. S., Karberg, N. J., King, J. S. & Giardina, C. P. (2003): Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels. Nature 425, 705-707.

Lukac, M., Lagomarsino, A., Moscatelli, M. C., De Angelis, P., Cotrufo, M. F. & Godbold, D. L. (2009): Forest soil carbon cycle under elevated CO2 - a case of increased throughput? Forestry 82, 75-86.

Maiermaercker, U. (1997): Experiments on the water balance of individual attached twigs of picea abies (l) karst in pure and ozone-enriched air. Trees-Struc.Funct. 11, 229-239.

Manes, F., Incerti, G., Salvatori, E., Vitale, M., Ricotta, C. & Costanza, R. (2012): Urban ecosystem services: tree diversity and stability of tropospheric ozone removal. Ecological Applications 22, 349-360.

Mansfield, T. A. (1998): Stomata and plant water relations: does air pollution create problems? Environmental Pollution 101, 1-11.

Mansfield, T. A. & Pearson, M. (1996): Disturbances in stomatal behaviour in plants exposed to air pollution. In Plant Response to Air Pollution (ed. by M. Yunus &M. Iqbal), John Wiley & Sons Lt, pp. 179-193.

Matyssek, R. & Sandermann, H. (2003): Impact of ozone on trees: an ecophysiological perspective. Progress in Botany 64 64, 349-404.

Matyssek, R., Sandermann, H., Wieser, G., Booker, F., Cieslik, S., Musselman, R. & Ernst, D. (2008): The challenge of making ozone risk assessment for forest trees more mechanistic. Environmental Pollution 156, 567-582.

Matyssek, R., Karnosky, D. F., Wieser, G., Percy, K., Oksanen, E., Grams, T. E. E., Kubiske, M., Hanke, D. & Pretzsch, H. (2010a): Advances in understanding ozone impact on forest trees: Messages from novel phytotron and free-air fumigation studies. Environmental Pollution 158, 1990-2006.

Matyssek, R., Wieser, G., Ceulemans, R., Rennenberg, H., Pretzsch, H., Haberer, K., Loew, M., Nunn, A. J., Werner, H., Wipfler, P., Osswaldg, W., Nikolova, P., Hanke, D. E., Kraigher, H., Tausz, M., Bahnweg, G., Kitao, M., Dieler, J., Sandermann, H., Herbinger, K., Grebenc, T., Blumenroether, M., Deckmyn, G., Grams, T. E. E., Heerdt, C., Leuchner, M., Fabian, P. & Haeberle, K. H. (2010b): 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.

McFrederick, Q. S., Kathilankal, J. C. & Fuentes, J. D. (2008): Air pollution modifies floral scent trails. Atmospheric Environment 42, 2336-2348.

McFrederick, Q. S., Fuentes, J. D., Roulston, T., Kathilankal, J. C. & Lerdau, M. (2009): Effects of air pollution on biogenic volatiles and ecological interactions. Oecologia 160, 411-420.

McLaughlin, S. B., Wullschleger, S. D., Sun, G. & Nosal, M. (2007a): Interactive effects of ozone and climate on water use, soil moisture content and streamflow in a southern Appalachian forest in the USA. New Phytologist 174, 125-136.

McLaughlin, S. B., Nosal, M., Wullschleger, S. D. & Sun, G. (2007b): Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. New Phytologist 174, 109-124.

Mills, G., Hayes, F., Wilkinson, S. & Davies, W. J. (2009): Chronic exposure to increasing background ozone impairs stomatal functioning in grassland species. Global Change Biology 15, 1522-1533.

Mills, G., Buse, A., Gimeno, B., Bermejo, V., Holland, M., Emberson, L. & Pleijel, H. (2007): A synthesis of AOT40-based response functions and critical levels of ozone for agricultural and horticultural crops. Atmospheric Environment 41, 2630-2643.

Mina, U., Kumar, P. & Varshney, C. K. (2010): Effect of ozone exposure on growth, yield and isoprene emission from tomato (Lycopersicon esculentum L.) plants. Vegetable Crops Research Bulletin 72, 35-48.

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.

Morgan, P. B., Mies, T. A., Bollero, G. A., Nelson, R. L. & Long, S. P. (2006): Season-long elevation of ozone concentration to projected 2050 levels under fully open-air conditions substantially decreases the growth and production of soybean. New Phytologist 170, 333-343.

Novak, K., Schaub, M., Fuhrer, J., Skelly, J. M., Hug, C., Landolt, W., Bleuler, P. & Krauchi, N. (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.

Ollinger, S. V., Aber, J. D. & Reich, P. B. (1997): Simulating ozone effects on forest productivity: Interactions among leaf-, canopy-, and stand-level processes. Ecological Applications 7, 1237-1251.

Pääkkönen, E., Vahala, J., Pohjolai, M., Holopainen, T. & Kärenlampi, L. (1998): Physiological, stomatal and ultrastructural ozone responses in birch (Betula pendula Roth.) are modified by water stress. Plant Cell and Environment 21, 671-684.

Paoletti, E. (2007): Ozone impacts on forests. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2, 13 pp.

Paoletti, E. & Grulke, N. E. (2005): Does living in elevated CO2 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.

Paoletti, E., Nali, C. & Lorenzini, G. (2007): Early responses to acute ozone exposure in two Fagus sylvatica clones differing in xeromorphic adaptations: Photosynthetic and stomatal processes, membrane and epicuticular characteristics. Environmental Monitoring and Assessment 128, 93-108.

Pellegrini, E., Nali, C. & Lorenzini, G. (2013): Ecophysiology of Tilia americana under ozone fumigation. Atmospheric Pollution Research 4, 142-146.

Pellegrini, E., Cioni, P. L., Francini, A., Lorenzini, G., Nali, C. & Flamini, G. (2012): Volatiles Emission Patterns in Poplar Clones Varying in Response to Ozone. Journal of Chemical Ecology 38, 924-932.

Penuelas, J., Llusia, J. & Gimeno, B. S. (1999): Effects of ozone concentrations on biogenic volatile organic compounds emission in the Mediterranean region. Environmental Pollution 105, 17-23.

Pinto, D. M., Nerg, A.-M. & Holopainen, J. K. (2007a): The role of ozone-reactive compounds, terpenes, and green leaf volatiles (GLVs), in the orientation of Cotesia plutellae. Journal of Chemical Ecology 33, 2218-2228.

Pinto, D. M., Blande, J. D., Souza, S. R., Nerg, A. M. & Holopainen, J. K. (2010): Plant Volatile Organic Compounds (VOCs) in Ozone (O-3) Polluted Atmospheres: The Ecological Effects. Journal of Chemical Ecology 36, 22-34.

Pinto, D. M., Blande, J. D., Nykanen, R., Dong, W.-X., Nerg, A.-M. & Holopainen, J. K. (2007b): Ozone degrades common herbivore-induced plant volatiles: Does this affect herbivore prey location by predators and parasitoids? Journal of Chemical Ecology 33, 683-694.

Pleijel, H., Danielsson, H., Simpson, D. & Mills, G. (2014): Have ozone effects on carbon sequestration been overestimated? A new biomass response function for wheat. Biogeosciences 11, 4521-4528.

Pleijel, H., Danielsson, H., Vandermeiren, K., Blum, C., Colls, J. & Ojanpera, K. (2002): Stomatal conductance and ozone exposure in relation to potato tuber yield - results from the European CHIP programme. European Journal of Agronomy 17, 303-317.

Pleijel, H., Ojanpera, K., Danielsson, H., Sild, E., Gelang, J., Wallin, G., Skärby, L. & Sellden, G. (1997): Effects of ozone on leaf senescence in spring wheat - Possible consequences for grain yield. Phyton-Annales Rei Botanicae 37, 227-232.

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

Pregitzer, K. S., Burton, A. J., King, J. S. & Zak, D. R. (2008): Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric Co-2 and tropospheric O-3. New Phytologist 180, 153-161.

Rämö, K., Kanerva, T., Ojanperä, K. & Manninen, S. (2007): Growth onset, senescence, and reproductive development of meadow species in mesocosms exposed to elevated O-3 and CO2. Environmental Pollution 145, 850-860.

Ren, W. & Tian, H. Q. (2007): Effects of ozone pollution on terrestrial ecosystem productivity. Zhiwu Shengtai Xuebao 31, 219-230.

Ren, W., Tian, H. Q., Liu, M. L., Zhang, C., Chen, G. S., Pan, S. F., Felzer, B. & Xu, X. F. (2007): Effects of tropospheric ozone pollution on net primary productivity and carbon storage in terrestrial ecosystems of China. Journal of Geophysical Research-Atmospheres 112, DOI: 10.1029/2007jd008521.

Ren, W., Tian, H. Q., Tao, B., Chappelka, A., Sun, G., Lu, C. Q., Liu, M. L., Chen, G. S. & Xu, X. F. (2011): Impacts of tropospheric ozone and climate change on net primary productivity and net carbon exchange of China's forest ecosystems. Global Ecology and Biogeography 20, 391-406.

Robinson, M., Heath, J. & Mansfield, T. (1998): Disturbances in stomatal behaviour caused by air pollutants. Journal of Experimental Botany 49, 461-469.

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

Sarkar, A. & Agrawal, S. B. (2012): Evaluating the response of two high yielding Indian rice cultivars against ambient and elevated levels of ozone by using open top chambers. Journal of Environmental Management 95, S19-S24.

Schoene, K., Franz, J. T. & Masuch, G. (2004): The effect of ozone on pollen development in Lolium perenne L. Environmental Pollution 131, 347-354.

Shi, G. Y., Yang, L. X., Wang, Y. X., Kobayashi, K., Zhu, J. G., Tang, H. Y., Pan, S. T., Chen, T., Liu, G. & Wang, Y. L. (2009): Impact of elevated ozone concentration on yield of four Chinese rice cultivars under fully open-air field conditions. Agriculture Ecosystems & Environment 131, 178-184.

Simpson, D., Arneth, A., Mills, G., Solberg, S. & Uddling, J. (2014): Ozone — the persistent menace: interactions with the N cycle and climate change. Current Opinion in Environmental Sustainability 9–10, 9-19.

Singh, E., Tiwari, S. & Agrawal, M. (2009): Effects of elevated ozone on photosynthesis and stomatal conductance of two soybean varieties: a case study to assess impacts of one component of predicted global climate change. Plant Biology 11, 101-108.

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-U4.

Sun, G., McLaughlin, S. B., Porter, J. H., Uddling, J., Mulholland, P. J., Adams, M. B. & Pederson, N. (2012): Interactive influences of ozone and climate on streamflow of forested watersheds. Global Change Biology 18, 3395-3409.

Talhelm, A. F., Pregitzer, K. S. & Zak, D. R. (2009): Species-specific responses to atmospheric carbon dioxide and tropospheric ozone mediate changes in soil carbon. Ecology Letters 12, 1219-1228.

Talhelm, A. F., Pregitzer, K. S. & Giardina, C. P. (2012): Long-Term Leaf Production Response to Elevated Atmospheric Carbon Dioxide and Tropospheric Ozone. Ecosystems 15, 71-82.

Talhelm, A. F., Pregitzer, K. S., Kubiske, M. E., Zak, D. R., Campany, C. E., Burton, A. J., Dickson, R. E., Hendrey, G. R., Isebrands, J. G., Lewin, K. F., Nagy, J. & Karnosky, D. F. (2014): Elevated carbon dioxide and ozone alter productivity and ecosystem carbon content in northern temperate forests. Global Change Biology 20, 2492-2504.

Tiiva, P., Rinnan, R., Holopainen, T., Morsky, S. K. & Holopainen, J. K. (2007): Isoprene emissions from boreal peatland microcosms; effects of elevated ozone concentration in an open field experiment. Atmospheric Environment 41, 3819-3828.

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

Topa, M. A., Vanderklein, D. W. & Corbin, A. (2001): Effects of elevated ozone and low light on diurnal and seasonal carbon gain in sugar maple. Plant Cell and Environment 24, 663-677.

Uddling, J., Teclaw, R. M., Pregitzer, K. S. & Ellsworth, D. S. (2009): Leaf and canopy conductance in aspen and aspen-birch forests under free-air enrichment of carbon dioxide and ozone. Tree Physiology 29, 1367-1380.

Uddling, J., Teclaw, R. M., Kubiske, M. E., Pregitzer, K. S. & Ellsworth, D. S. (2008): Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. Tree Physiology 28, 1231-1243.

Van Dingenen, R., Dentener, F. J., Raes, F., Krol, M. C., Emberson, L. & Cofala, J. (2009): The global impact of ozone on agricultural crop yields under current and future air quality legislation. Atmospheric Environment 43, 604-618.

VanLoocke, A., Betzelberger, A. M., Ainsworth, E. A. & Bernacchi, C. J. (2012): Rising ozone concentrations decrease soybean evapotranspiration and water use efficiency whilst increasing canopy temperature. New Phytologist 195, 164-171.

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.

Vuorinen, T., Nerg, A. M. & Holopainen, J. K. (2004): Ozone exposure triggers the emission of herbivore-induced plant volatiles, but does not disturb tritrophic signalling. Environmental Pollution 131, 305-311.

Vuorinen, T., Nerg, A. M., Vapaavuori, E. & Holopainen, J. K. (2005): Emission of volatile organic compounds from two silver birch (Betula pendula Roth) clones grown under ambient and elevated CO2 and different O-3 concentrations. Atmospheric Environment 39, 1185-1197.

Wagg, S., Mills, G., Hayes, F., Wilkinson, S. & Davies, W. J. (2013): Stomata are less responsive to environmental stimuli in high background ozone in Dactylis glomerata and Ranunculus acris. Environmental Pollution 175, 82-91.

Wang, X. P. & Mauzerall, D. L. (2004): Characterizing distributions of surface ozone and its impact on grain production in China, Japan and South Korea: 1990 and 2020. Atmospheric Environment 38, 4383-4402.

Wang, X. Z. & Taub, D. R. (2010): Interactive effects of elevated carbon dioxide and environmental stresses on root mass fraction in plants: a meta-analytical synthesis using pairwise techniques. Oecologia 163, 1-11.

Wieser, G. & Matyssek, R. (2007): Linking ozone uptake and defense towards a mechanistic risk assessment for forest trees. New Phytologist 174, 7-9.

Wilkinson, S. & Davies, W. J. (2010): Drought, ozone, ABA and ethylene: new insights from cell to plant to community. Plant Cell and Environment 33, 510-525.

Winwood, J., Pate, A. E., Price, A. J. & Hanke, D. E. (2007): Effects of long-term, free-air ozone fumigation on the cytokinin content of mature beech trees. Plant Biology 9, 265-278.

Wittig, V. E., Ainsworth, E. A. & Long, S. P. (2007): To what extent 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.

Wittig, V. E., Ainsworth, E. A., Naidu, S. L., Karnosky, D. F. & Long, S. P. (2009): Quantifying the impact of current and future tropospheric ozone on tree biomass, growth, physiology and biochemistry: a quantitative meta-analysis. Global Change Biology 15, 396-424.

Xu, H., Chen, S. B., Biswas, D. K., Li, Y. G. & Jiang, G. M. (2009): Photosynthetic and yield responses of an old and a modern winter wheat cultivars to short-term ozone exposure. Photosynthetica 47, 247-254.

Yuan, J. S., Himanen, S. J., Holopainen, J. K., Chen, F. & Stewart, C. N. (2009): Smelling global climate change: mitigation of function for plant volatile organic compounds. Trends in Ecology & Evolution 24, 323-331.

Zhang, W. W., Niu, J. F., Wang, X. K., Tian, Y., Yao, F. F. & Feng, Z. Z. (2011): Effects of ozone exposure on growth and photosynthesis of the seedlings of Liriodendron chinense (Hemsl.) Sarg, a native tree species of subtropical China. Photosynthetica 49, 29-36.

Zhu, X. K., Feng, Z. Z., Sun, T. F., Liu, X. C., Tang, H. Y., Zhu, J. G., Guo, W. S. & Kobayashi, K. (2011): Effects of elevated ozone concentration on yield of four Chinese cultivars of winter wheat under fully open-air field conditions. Global Change Biology 17, 2697-2706.

7 Field observations and case studies

With the exception of some studies comparing responses of plants in filtered and unfiltered ambient air, there is one important fact the previous chapters of this study have in common: In order to simulate future pollution scenarios they describe a potential impact of ozone on ecosystems which might occur if ozone levels would be elevated. In this chapter all observations will be compiled that contribute to the question whether current or past ozone exposure scenarios already have or had an impact on complex ecosystems and their constituents or not.

With the raising awareness of noticeable symptoms of forest damage several national and international monitoring and research programs have been initiated in the 1970s (USA) and 1980s (Europe), respectively, to assess both the extent of ecosystem impacts and their causal agents. Over time, the forest health monitoring activities have been extended while estimating the threat posed by the exposure to ozone became an important objective. At a national and international scale long-range programmes are the ‘*Forest Health Monitoring (FHM)*’ of the U.S. Environmental Protection Agency and the USDA Forest Service or the ‘*International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests)*’ of the UNECE. In addition, a number of national or regional case studies and multidisciplinary research programs have been initiated e.g. the ‘*National Forest Response Program*’, the ‘*San Bernardino Mountains Network Study (SBM)*’ and the ‘*The Vital Signs Program of the U.S. National Park Service*‘ of the USA or the ‘*CONECOFOR (CONtrolli ECOsistemi FORestali)*’ in Italy and the ‘*International Long-Term Ecological Studies in the Carpathian Mountains*‘ in Europa.

Table 16: Summary of publications related to the issue ‘Field observations and case studies’. Number of publications grouped according to geographical and chronological relevance.

subject	total	before 2000	2000-2010	after 2010
FOREST CONDITION	**115**	**61**	**48**	**6**
general	10	5	5	0
America	16	7	8	1
Asia	4	0	1	3
Europe (incl. ICP-Forests)	85	49	34	2
CASE STUDIES AMERICA	**151**	**93**	**54**	**4**
San Bernardino	77	53	24	0
Sierra Nevada	19	12	7	0
East and Northeast of USA	42	22	16	4
Central-America	13	6	7	0
CASE STUDIES EUROPE	**79**	**5**	**65**	**9**
Italy (CONECOFOR)[$]	20	0	20	0
Carpathian Mountains	47	5	37	5
Lithuania	12	0	8	4

[$] National Integrated Programme for Forest Ecosystem Monitoring (Italian acronym: CONtrolli ECOsistemi FORestali)

The majority of relevant studies has been published before 2000 and covered results of the SBM study since the 1970s and reports on the forest condition in the USA and Europe since the 1980s, whereas case studies performed in Europe (Italy and Central-Europe) are of recent date (Table 16).

7.1 Ozone-specific foliar injury on native plants

This chapter aims to give an overview of worldwide activities to assess the incidence of ozone-specific injuries on natural vegetation and more integrative ecosystem parameters, if available. This includes all field observations, which comprise ozone exposure levels and their effects at the ecosystem level. With regard to the high level of causality and the easy feasibility the repeated assessment of ozone specific symptoms of foliar injuries has been proved highly successful. Experimental verification of symptoms (Skelly et al. 1999; Bussotti et al. 2003c; Vollenweider et al. 2003; Gravano et al. 2004; Kline et al. 2008) and publication of pictorial guides (Jacobson & Hill 1971; Sanchez Gimeno et al. 1992; Innes et al. 2001) completed by special courses of symptom recognition conduced to the success of this generally accepted monitoring method[4].

Table 17: Number of species which are proven to exhibit symptoms of ozone-specific foliar injury in the field.

continent	no. of species
Central America	10
Europe	182
North America	58
Asia	15
total	**258**

For species list see Annex table 12.

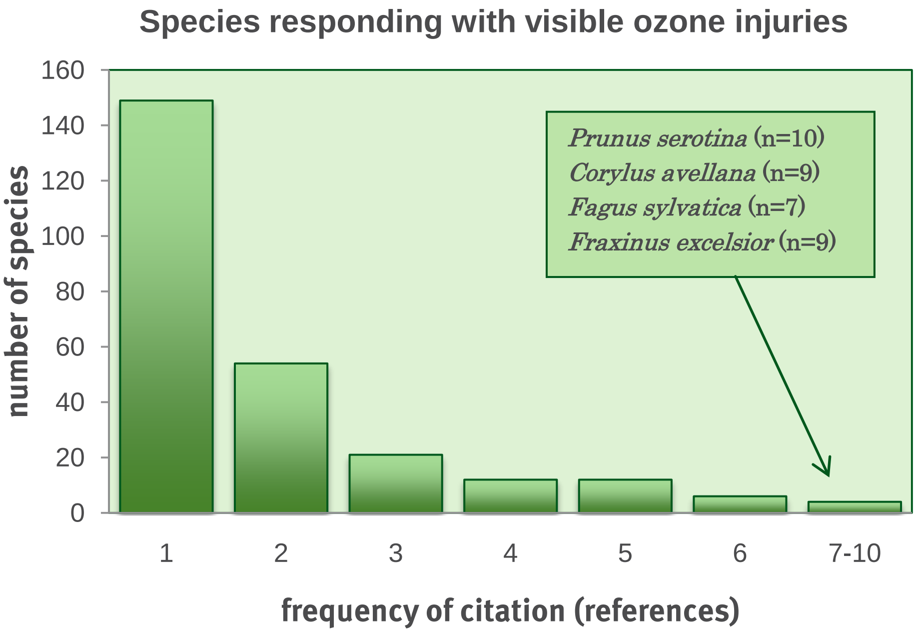
In this way, for Europe, North and Central America, and Asia a total number of 258 woody and herbaceous plant species belonging to the native flora has been recognised to exhibit specific foliar symptoms in the field in response to ambient ozone levels (Table 17 and Annex Table 12). Out of these, there are 55 species, whose impairment by ambient ozone has been evidenced by three studies at least. The species cited most frequently are *Corylus avellana, Fagus sylvatica, Fraxinus excelsior,* and *Prunus serotina* (Figure 2).

Although the significance of the parameter 'visible leaf injury' in indicating effects on biodiversity of an ecosystem has to be discussed, its relevance should not be discounted as the expression of such symptoms clearly indicate the presence of any kind of impairment. Moreover, an assessment of species-specific responses and their temporal and spatial variation by long-term observations may allow deducing valuable information about the risk for biodiversity and the fate of sensitive genotypes. Secondly, foliar injury and premature leaf fall is thought to decrease photosynthetic capacity and therefore may suppress radial growth and reduce nutrient retention in green biomass (Miller 1985).

---

[4] http://www.wsl.ch/ozone/ICP-Forests_2001.ehtml
http://www.wsl.ch/ozone/ICP-Forests_2003.ehtml
http://www.ozone.wsl.ch/index-en.ehtml

Figure 2: Number of species exhibiting symptoms of ozone-specific foliar injury in the field. Frequency distribution of records for individual species documented in the literature (total n = 258).



7.2 Field surveys USA and Canada

Based on ozone data recorded since 1974 it has been suggested that the Pacific Northwest and Atlantic Northeast have the greatest potential for tree damage (McBride & Miller 1987) and for example in California ozone injury was consistently detected at many sites in 2000 and 2005 (Christensen et al. 2008).

The long-term nationwide biomonitoring program (‘U.S. Forest Health Monitoring Program’ FHM) allows quantifying regional trends in ozone stress. The results of the field surveys resulted in a map for plant health risk from ozone. The findings reported in this paper focus on the field measurements collected across the northeast from 1996 through 2000. The results show a strong regional correlation between biomonitoring data and air quality data from physical ozone monitors. In any year, there is a higher percentage of ozone injured plants with more severe symptoms in areas with relatively high ozone concentrations than in areas with relatively low ozone (Smith et al. 2003).

The National Park Service is concerned about the effects on plants and ecosystems in a number of parks. For the 244 U.S. National Parks for which detailed ozone risk assessments were conducted (The Vital Signs program of the U.S. National Park Service), the risk of foliar injury was high in 65 parks, moderate in 46 parks, and low in 131 parks (Kohut 2007).

Table 18 is listing 29 species on which ozone-specific and ozone-like symptoms have been recorded in eight different National Parks across the USA.

Table 18: Species exhibiting ozone-specific and ozone-like symptoms recorded in different National Parks in USA.

species	**site location**	**park**	**time period**	**Reference**
Abies concolor	west	SNFP	1974	Williams et al. (1977), Williams & MacGregor (1975)
Ailanthus altissima	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
Apocynum androsaemifolium	east	MoNW	1998-2000,2002-2004	Davis (2007b)
	north east	SeNW	1999-2004	Davis (2007a)
Asclepias exaltata	east	GSMP	1992-1996	Chappelka et al. (2007)
	east	GSMP	2000, 2001	Souza et al. (2006)
Asclepias syriaca	north east	SeNW	1999-2004	Davis (2007a)
	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
	east	GSMP	1992	Chappelka et al. (1997)
	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)
Calocedrus decurrens	west	SNFP	1977	Williams et al. (1977)
Cornus florida	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)
Corylus cornuta	east	MoNW	1998-2000,2002-2004	Davis (2007b)
Fraxinus americana	east	SNP	1991-1993	Hildebrand et al. (1996)
Fraxinus spp.	east	MoNW	1998-2000,2002-2004	Davis (2007b)
Liquidambar sp.	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)
Liriodendron tulipifera	east	GSMP	1991-1993	Chappelka et al. (1999a)
	east	SNP	1991-1993	Hildebrand et al. (1996)
Parthenocissus quinquefolia	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
Pinus contorta	west	SNFP	1978	Williams et al. (1977)
Pinus lambertiana	west	SNFP	1975	Williams et al. (1977), Williams & MacGregor (1975)
Pinus ponderosa	west	SNFP	1979	Williams et al. (1977)
	west	SNFP	1991-1994	Miller et al. (1998a)
Pinus jeffreyi	west	SNFP		Williams & MacGregor (1975)
	west	SNFP	1991-1994	Miller et al. (1998a)
Populus spp.	east	MoNW	1998-2000,2002-2004	Davis (2007b)
Prunus pensylvanica	east	MoNW	1998-2000,2002-2004	Davis (2007b)
Prunus serotina	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
	east	GSMP	1991-1993	Chappelka et al. (1999b), (1999a)
	east	GSMP	1992	Chappelka et al. (1997)
	east	SNP	1991-1993	Chappelka et al. (1999b), Hildebrand et al. (1996)
	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)
	east	MoNW	1998-2000,2002-2004	Davis (2007b)

species	site location	park	time period	Reference
	north east	SeNW	1999-2004	Davis (2007a)
Rhus copallina	east	CaRNW	1996-1998, 2002-2003	Davis (2009)
	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
Rudbeckia laciniata	east	GSMP	2001	Davison et al. (2003)
	east	GSMP	2000, 2001	Chappelka et al. (2003)
Sambucus canadensis	north east	SeNW	1999-2004	Davis (2007a)
Sapium sebiferum	east	CaRNW	1996-1998, 2002-2003	Davis (2009)
Sassafras albidum	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
	east	GSMP	1991-1993	Chappelka et al. (1999a)
	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)
Sequoiadendron giganteum	west	SNFP	1976	Williams et al. (1977)
Verbesina occidentalis	east	GSMP	2000, 2001	Chappelka et al. (2003)
Viburnum nudum	east	MoNW	1998-2000,2002-2004	Davis (2007b)
	north east	SeNW	1999-2004	Davis (2007a)
Vitis sp.	east	CaRNW	1996-1998, 2002-2003	Davis (2009)
	east	FoNW	1993-1996, 2001-2003	Davis & Orendovici (2006)
	south east	MiNW	1998, 2000, 2003, 2004	Davis (2011)

CaRNW (Cape Romain National Wildlife Refuge)
FoNW (Forsythe National Wildlife Refuge)
GSMP (Great Smoky Mountains National Park)
MiNW (Mingo National Wildlife Refuge)
MoNW (Moosehorn National Wildlife Refuge)
SeNW (Seney National Wildlife Refuge)
SNFP (Sequoia National Forest and the Sequoia-Kings Canyon National Park)
SNP (Shenandoah National Park)

7.2.1 Canada

Miller & Watmough (2009) studied 35 hardwood forest plots dominated by sugar maple (*Acer saccharum*) along a contrasting climate, soil acidity, and air pollution gradient in southern Ontario. Neither for vegetation species richness or diversity nor for forest health a correlation was found with indices of air pollution, climate, or soil acidity. However, foliose lichen species richness was negatively correlated with modelled air pollution levels (S deposition, N deposition, and atmospheric ozone).

7.2.2 USA - Eastern coast and Appalachian

Several field surveys were conducted within National Wildlife Refuges or National parks, e.g. Great Smoky Mountain National Park, Shenandoah National Park, Moosehorn National Wildlife Refuge, and Acadia National Park to determine whether ozone-induced symptoms occurred on refuge vegetation. Both, The Acadia National Park (Harris et al. 2012) and The Great Smoky Mountain National Park (Chappelka et al. 1999a) were described as refuges with a wide diversity of plant and both experienced some of the highest concentrations of ozone in eastern North America (Harris et al. 2012) with more periods of high peak values were measured at higher elevations (Neufeld et al. 1992).

Increased ozone concentrations have been reported in the Blue Ridge Mountains of Virginia since the late 1970s with a monthly average of up to 59 ppb (Duchelle et al. 1982) and is found to be responsible for an increase in foliar injury symptoms and litter fall rates on eastern white pine *(Pinus strobus,* Skelly & Johnston 1977; Swank & Vose 1990). Moreover, using dendro-chronological measurements a decline in overall growth has been related to ozone as annual mean increment growth in the 1974-1978 period was 51 % less than during the 1955-1959 period (Benoit et al. 1982). For *Liriodendron tulipifera* and *Prunus serotina* reduced growth of trees exhibiting visible foliar injury relative to non-injured individuals was noticed but differences were not significant (Somers et al. 1998).

Mostly, ozone specific symptoms of leaf injury were observed on ozone-sensitive bioindicators during each survey year, but the incidence (percentage) of plants exhibiting symptoms varied among species and years (Davis 2007b; a), aspect (Chappelka et al. 1997), or populations (Davison et al. 2003). Especially soil moisture and other micro-site and environmental factors are thought to interact with ozone (Lefohn et al. 1997; Chappelka et al. 1999a).

However, it is likely that in most years the ambient ozone levels at the most sites are high enough to cause injury on sensitive refuge plants (Davis 2007b). As early as in 1980 (Duchelle et al. 1983) demonstrated the high potential of ambient ozone concentrations to reduce biomass production on the native vegetation by the use of air filtration. Recent studies indicate that ambient levels of ozone in the Great Smoky Mountains National Park (Neufeld et al. 2012) and the southern Appalachian (McLaughlin et al. 2007) can adversely affect physiological parameters such as water use efficiency or limit growth of mature forest trees in sensitive plants.

7.2.3 USA - Central and west

Kohut et al. (2012) reported on surveys for foliar ozone injury in the Rocky Mountain National Park, Colorado, from 2006 through 2010. Ozone-specific symptoms were found on *Rudbeckia laciniata* each year whereas *Apocynum androsaemifolium* and *Populus tremuloides* were found to be unresponsive at this site.

7.2.4 USA - Western coast

Besides the San Bernardino Mountains the mixed conifer forest type in the **Sierra Nevada** has become the major focus of investigations because of the incidence of ozone injury on ponderosa and Jeffrey pines (Williams & MacGregor 1975; Miller et al. 1996) or growth reductions (Peterson et al. 1991). Therefore, the USDA Forest Service and USDI National Park Service established permanent plots to monitor potential ozone damage on this forest ecosystem.

Although montane forests of the southern Sierra Nevada are relatively distant from urban areas, they receive moderately high concentrations of ozone during the summer months (50 – 70 ppb, 24-h average, 1988-1994, Takemoto et al. 2001), forming a general gradient from north to south (Peterson et al. 1987; Peterson et al. 1995).

Injury to the mixed conifer forest from tropospheric ozone has occurred in the Sierra Nevada since the 1970s (Arbaugh et al. 1998). In addition to the occurrence of leaf injury symptoms on *Pinus ponderosa* and *Pinus Jeffrey* (Peterson et al. 1987; Peterson et al. 1995; Weinstein et al. 2005), symptom expression has been described for at least six more species (see Table 18, SNFP, (Williams & MacGregor 1975; Williams et al. 1977) while amounts of visible injury has been assessed to be greater in the southern than in the central or northern Sierra Nevada. In general, symptom intensity in the Sequoia area was lower than in the San Bernardino Mountains (Peterson & Arbaugh 1988; Miller et al. 1998a; Weinstein et al. 2005). However, growth reductions caused by ozone ranged from none (Peterson & Arbaugh 1988) to a reduction in mean annual radial increment by 11 percent per year calculated for symptomatic trees (Peterson *et al.*, 1987) with old and large trees having been impacted most.

7.2.5 The San Bernardino Mountains Gradient Study

The San Bernardino National Mountain Forest located north and east of the Los Angeles basin in Southern California, USA, has become a synonym for the most encompassing investigation of ozone impacts of ground level ozone on a forest ecosystem. During the second half of the 20th century, the forests of the San Bernardino Mountains have been exposed to some of the highest rates of N and ozone deposition of any forest ecosystem in the world (Allen et al. 2007). Thus, an extensive decades-long multidisciplinary study using the San Bernardino Mountains as a natural "laboratory" resulted in a well-documented evidence of multiple ecosystem effects in the field caused by elevated ozone concentrations. Kickert & Krupa (1990) characterised these results as "probably the most comprehensive data collection and analysis performed for a forest under ambient field exposure". Moreover, the perception and ongoing investigation of the phytotoxic potential of the air pollution compound ozone was initiated when unexplainable symptoms of decline has been observed on native pines in the San Bernardino Mountains in the mid-1950s, followed by the verification of its ability of being induced by ozone by Miller et al. (1963).

The first symptom of damage to Ponderosa pine (*Pinus ponderosa*) was reported in 1953. These symptoms included a kind of chlorotic mottling of the needles, together with a loss of all but the current season's needles, and a reduction in number and size of remaining needles (McBride et al. 1975; Miller et al. 1977; Bytnerowicz et al. 2007).

In 1972, the U.S. Environmental Protection Agency, in cooperation with the University of California and the U.S. Forest Service, initiated a study on the effects of oxidant air pollutants on the mixed conifer forest ecosystem in the San Bernardino Mountains. Beginning in 1991 a follow-up study was initiated under the sponsorship of the California Air Resources Board. All scientific activities were related to a series of permanent monitoring plots which were established along an air pollution gradient (McBride & Laven 1999). An introduction to the structure and experimental design of the multidisciplinary study and summary of the mean findings of 16 investigators is given by Miller (1985). As early as in 1977, in the USA a report was published reporting on the activities of twelve scientists representing several research disciplines which have "collaborated in integrated studies to determine the chronic effects of photochemical oxidant air pollutants on a mixed conifer forest ecosystem" (Miller et al. 1977). From a present-day perspective, the SBM monitoring sites represent some of the oldest forest air-pollution effect sites in the world and, therefore, are a resource of great importance to research activities (Arbaugh et al. 2003).

7.2.5.1 Site description

The San Bernardino National Forest is managed for recreation, wildlife, watersheds, and other ecosystem and aesthetic values (Pronos et al. 1999). Details of location, topography, geology and soils, climate and ozone pollution and its vegetation can be found at Miller (1985). Vegetation in the San Bernardino Mountains is composed about equally of chaparral and forest types (Miller et al. 1977) of remarkable diversity (Minnich 1999). The high productive ecosystems of the southern escarpment and crest of SBM are subjected to the highest air pollution concentrations in summer due to the advection of marine air from the Los Angeles Basin as a consequence of onshore flow and anabatic circulations (Minnich 1999). Dominant tree species include ponderosa and Jeffrey pine (*Pinus ponderosa* and *Pinus jeffreyi*) and white fir (*Abies concolor,* Miller et al. 1977). The effect of slope and aspect on tree growth is magnified by Mediterranean climate (Arbaugh et al. 1999).

7.2.5.2 “San Bernardino Mountains Gradient Study (SBGS) network”

In 1972, the San Bernardino Mountains Gradient Study (SBGS) network was initiated to investigate the effects of exposure to ozone on a pine and mixed conifer forest of the San Bernardino Mountains. All of the experimental work was done in the coniferous forest zone between 1525 and 2365 m comprising five forest types with differing dominance of ponderosa or Jeffrey pine (Miller 1985). Eighteen permanent observation plots were established in the SBM along the air quality gradient from west to east that traverse the extremes of ozone exposures.

From 1973 to 1978, this interdisciplinary study focussed on changes in four ecosystem processes: The flows of water, carbon and nutrients, and patterns of diversity in time and space (Miller 1985). Tree condition of pines was measured annually, later on, a long-term observation was kept up until 1994 using selected sub-plots (Fenn & Dunn 1989; Temple et al. 2005). Monitoring of biological data included for example tree population dynamics, stand-tree growth, stand mortality response, tree seedling establishment, cone and seed production, litter production and litter decomposition. All data should have been discussed in relation to the factors climate, natural topography, and soil types and characteristics (Miller et al. 1977).

Limitation of this approach has been reflected by the following observations: The gradient in environmental conditions did not exclusively exist for ozone. Moreover, a gradient was also present for precipitation as well as elevation is increasing from west to east and sites differed in several soil parameters (total N, soil carbon, pH, litter, Allen et al. 2007). In terms of tree population dynamics, it has been observed that there was more variation in forest composition than expected. Thus, Miller et al. (1977) stated that the 18 plots represent an inadequate sample to establish the relationship between air pollution injury and successional change, and because of the dissimilarity in composition of the forest stands the predictive capability of a simple stand succession mode to describe tree population dynamics is limited.

7.2.5.3 Climatic parameters and pollution exposure

In the vicinity of the Los Angeles Metropolitan concentrations of ozone have been increased since the 1950s with peak values in the 1970s. A broad and comprehensive description of the exceptional events in the Mixed Conifer Forest of San Bernardino Mountains is given by Temple et al. (2005): The concentrations of air pollutants arose as a consequence of a unique set of topographic and climatological factors resulting in the formation of a subsidence inversion layer. These special conditions combined a high potential to form ozone, a typical inflow pattern of air pollution from the Los Angeles Basin eastward, an increase of elevation from coastal plain to the mountains height and were accompanied by an increase of inversion layer and temperatures given the particularity that the highest concentrations were found in mountain slopes at 1200 to 1500 m (Arbaugh et al. 1999). As a second characteristic, high ozone concentrations persist in the evening and early morning hours and therefore coincide with high values for humidity and physiological activity of vegetation.

Generally, a northeast to southwest gradient of increasing pollution across the mountain range existed (Fenn & Dunn 1989; Grulke et al. 1998; Bytnerowicz et al. 1999; Temple et al. 2005). In the 1970s the western site had 36 % higher ozone concentration than the eastern one (Allen et al. 2007). Ozone data recording started in 1963 documenting a continuing upward trend from 1963 in both peak ozone concentrations and in numbers of hours of elevated ozone in the SBM (Table 19). The highest hourly concentration ever recorded was 600 ppb on June 28, 1974 (National Research Council 1977). During the 1970s growing season means frequently exceeded 100 ppb for 10 or more hours daily (Miller & McBride 1975; Temple et al. 2005). However, in response to concerted air pollution control activities, ozone levels have declined steadily since the 1980s (Miller et al. 1997) Growing season ozone means in the late 1990s have declined to 50 to 60 ppb (Temple et al. 2005).

Table 19: Characteristics of ozone pollution in the San Bernardino Mountains, USA. max. = maximum, avg. = average, seas. = seasonal.

time period	index of ozone exposure				reference
	max. hourly	avg. peak	season mean	12h seas. mean	
1970s	600 ppb		›100 ppb		Bytnerowicz et al. (2008)
1970s		380 ppb			Temple et al. (2005)
1973-1978			100-120 ppb		Miller (1985)
1974	600 ppb	46 days › 330 ppb			Temple et al. (2005)
1990s	180 ppb		60 ppb		Bytnerowicz et al. (2008)
late 1990s	220 ppb		50-60 ppb		Temple et al. (2005)
				95 ppb (west)	Arbaugh et al. (1999)
				60 ppb (east)	Arbaugh et al. (1999)
2000			53-59 ppb		Alonso et al. (2002)
2002-2006			58-69 ppb*) (west)		Bytnerowicz et al. (2008)
2002-2006			44-50 ppb*) (east)		Bytnerowicz et al. (2008)

*) Range of 2-week means during season

In order to document the changing air quality conditions in the San Bernardino Mountains a historical database of hourly ozone concentrations for on specific site, Crestline, California has been reconstructed based on ozone monitoring data taken since 1963 and completed with data from the CARB (California Air Resources Board) database (Lee et al. 2003). While mean concentrations reached a plateau oscillating around 60–70 ppb starting in 1995 hourly maximum ozone concentrations showed a continuous decline during the following 25 years to about 150 ppb. However, various exposure indices measured during the summers of 2002 to 2006 reflected still a high potential of ozone phytotoxicity (AOT40 75 ppm h, Bytnerowicz et al. 2008).

7.2.5.4 Ozone effects

Main results of the 'San Bernardino Mountains Gradient Study' are summarised in Annex, Table 11.

7.2.5.4.1 Visible symptoms of foliar injury

Photochemical oxidant air pollution was first identified in 1962 to be responsible for the symptoms of the initially termed "x-disease" and in this way for the decline and death of ponderosa pine (*Pinus ponderosa*) trees in southern California (Miller 1973). In fact, these symptoms, that have been observed since the mid 1950s, could be related to ozone as a causing agent by means of controlled experiments using charcoal-filtered and ambient air

(Miller et al. 1963; Linzon 1966; Richards et al. 1968). Ozone injury symptoms of ponderosa pine include chlorotic mottle of needles, reduced needle length, and low needle retention (Miller, 1973; Pronos et al., 1978). Additionally, mottling was induced experimentally in three further species of pine: *P. canariensis*, *P. radiate* and *P. halepensis* (Linzon 1966; Richards et al. 1968), however among conifers native to the SBM, ponderosa and Jeffrey pines were the most susceptible to ozone (Temple et al. 2005)[5]. In summary, there were five tree species, six shrub species and twenty herbaceous plant species native to the SBM for which the expression of visible leaf injury has been described (Table 20).

Table 20: Species exhibiting ozone-specific and ozone-like symptoms recorded in the San Bernardino Mountains, USA.

shrubs and trees	reference	herbaceous plants	reference
Acer macrophyllum	Temple et al. (2005)[5]	*Artemisia dracunculus*	Temple (1999)
Amorpha californica	Miller et al. (1977); Temple (1999)	*Artemisisa douglasiana*	Miller et al. (1977); Temple (1999)
Cornus nuttallii	Temple (1999)	*Asclepias californica*	Temple (1999)
Pinus jeffreyi	Temple et al. (2005)[5]	*Asclepias fascicularis*	Temple (1999)
Pinus ponderosa	Fenn & Dunn (1989); Jones & Paine (2006)	*Bromus orcuttianus*	Miller et al. (1977)
Platanus racemosa	Temple et al. (2005)[1]	*Clarkia rhomboidea*	Temple (1999)
Prunus emerginata	Temple (1999)	*Collomis grandiflora*	Miller et al. (1977); Temple (1999)
Quercus kelloggii	Miller et al. (1977); Temple et al. (2005)[5]	*Cordylanthus rigidus*	Temple (1999)
Ribes ssp.	Temple (1999)	*Elymus glauca*	Miller et al. (1977)
Rubus parviflorus	Temple (1999)	*Erigeron breweri*	Miller et al. (1977)
Sambucus mexicana	Temple (1999)	*Gallium aparine*	Miller et al. (1977)
		Gayophytum diffusum	Temple (1999)
		Lepidium virginicum L. var. pubescens	Temple (1999)
		Oamorhiza chilense	Miller et al. (1977)
		Oenothera elata	Temple (1999)
		Potentilla glandulosa	Miller et al. (1977); Temple (1999)
		Silene verecunda	Miller et al. (1977)
		Solidago sp.	Miller et al. (1977)
		Tanacetum parthenium	Temple (1999)
		Vicia californica	Miller et al. (1977)

---

[5] citing Miller & McBride (1975)

Definitely for *Pinus ponderosa* it has been ascertained beyond doubt that trees from highly polluted western areas have shown greater symptoms caused by ozone exposure than trees from less impacted eastern areas (Miller 1985), recently summarised by Temple et al. (2005), Eatough Jones et al. (2004), and Jones & Paine (2006). Some other species, white fir and oaks, did show a gradient of foliar injury similar to pines, but both were less sensitive (Miller & Rechel 1999).

The re-assessment of the pine health in the 1990s clearly showed that the severity of ozone exposure is certainly less than in the 1970s but also indicated that a general pattern of decreasing crown damage from the southwest to the northeast still existed. A general improvement in crown conditions over the 20-year period was found for all plots except the plot with the highest amount of ozone injury and the highest input of ambient ozone (Miller & Rechel 1999; Temple et al. 2005).

7.2.5.4.2 Growth response of forest trees

First growth analyses of mature ponderosa pine trees have been made by Miller et al. (1977) and McBride et al. (1975): Annual ring widths of increment cores correlated weakly with the injury score of each tree, and experimental exclusion of pollutants allowed damaged pine trees not only to recover from foliar damage during five years but also to increase the amount of needle biomass and height growth. This experiment was able to show a difference of 26 % in height growth attributed to air pollution. Compared to annual radial growth calculated for the rings produced from 1910 to 1940 during the 30-year-period between 1944 and 1974 air pollution caused a 40 % reduction in radial growth. Furthermore, growth increment of ponderosa pine began to recover to pre-1945 levels between 1973 and 1991 (Miller & Arbaugh 2000), and growth trends going in the opposite direction of the ozone and crown damage gradients to trees have been recorded (Arbaugh et al. 1999). The authors attributed this trend to the fact that two other gradients occur along the transect: A decline in precipitation and a decrease in nitrogenous dry deposition.

In the 1990s similar investigations of basal growth have been done for *Pseudotsuga macrocarpa*. When differences in basal area increment growth (BAI) of periods with high ozone were compared to low ozone periods for more than 80 % of all trees growth reductions caused by ozone had been detected. Additionally, trees at sites with high-ozone exposure have larger growth decreases than at sites with low ozone (Peterson et al. 1995; Arbaugh et al. 1999). However, changes in growth and needle could not be related to any kind of ozone specific foliar symptom of ozone damage (Arbaugh et al. 1999). Grulke et al. (1998) investigated the fine and medium root biomass of *P. ponderosa* in the upper 40 cm of mineral soil and demonstrated that high foliar injury and lower foliar retention were accompanied by lower root biomass as a function of the gradient in long- term pollution deposition.

7.2.5.4.3 Tree mortality

Retrospectively, the decline of *P. ponderosa* and *P. jeffreyi* stands in the San Bernardino Mountains was probably the most obvious example of ozone-caused impacts on forests. Frequency of both tree mortality and beetle activity was higher at the high pollution site than at the low pollution site (Pronos et al. 1999; Eatough Jones et al. 2004), additionally, high mortality rates i.e. 33 % of the young mature ponderosa pine and 24 % for white fir occurred only on that group of plots showing severe foliar injury (McBride & Laven 1999). Weakened trees became more susceptible to other stressors resulting in large amounts of sanitary cuttings and harvesting between 1964 and 1984. As a result, accumulated pine mortality related to chronic foliar injury ranged from 0 to 8.9 % between 1973 and 1975 (Miller et al.

1977). Resurveyed plots from one site indicate that 25 % of ponderosa pines died between 1973 and 1992 (Arbaugh et al. 1999) as a result of severe ozone injury in combination with bark beetles, drought, and other natural stressors (Temple et al. 2005).

7.2.5.4.4 Plant species composition and succession

The selective removal of damaged pines has contributed to the change in species composition of the mixed conifer forest over the past 25 years: At sites with high ozone, N deposition and precipitation ozone and shade tolerant species (white fir and incense cedar) gained advantage over more susceptible species such as ponderosa pine (Arbaugh et al. 2003; Temple et al. 2005).

When ozone and other stressors have the potential to reduce the canopy leaf area of a stand allowing more solar irradiance to reach the forest floor they indirectly affect the micro-environment at the soil surface which in turn has an effect on seedling establishment (Binkley et al. 1992). More directly, stand initiation can be disturbed when cone production was reduced, what have been shown by (Luck 1980) for ozone-injured pine trees.

The flora of the SBM is particular rich and divers, nearly 25 % of all plant species in California grow here, numerous annual and perennial plants are endemic to these mountains (Temple 1999). Comparisons of the species lists from 1973 and 2003 suggested that major changes have occurred in the understory vegetation of the mixed conifer forest over the past 30 years. Atmospheric N pollution and ozone were not linearly related to herb cover or richness of the six sites observed, as would be expected in a multidimensional gradient. However, there was a clearly detrimental effect of air pollution at the two westernmost sites and both lost species since 1973 (Allen et al. 2007)

Beginning in 1996, assessments of foliar ozone injury symptoms have been made on selected plant species at 14 sites. For at least three species (*Sambucus mexicana, Gayophytum diffusum* and *Cordylanthus rigidus*) these observations indicated that ozone-susceptible genotypes have not been eliminated from the populations during the past 50 years (Temple 1999). The persistence of these ozone-susceptible genotypes of various plant species in areas of prevailingly high ambient ozone concentrations suggests that severe foliar ozone injury per se is not a sufficient selective pressure to alter significantly the genetic structure of these plant populations in the number of generations from the 1950s until present (Temple 1999).

7.2.5.4.5 Lichen communities

The use of lichens as indicators of air pollution, particularly SO_2, is well established, but in general lichens have not proved to be as sensitive as vascular plants to ozone (see chapter 3.5). The assumption that lichens may also respond to ozone is strengthened by the fact that gradients in oxidant levels, in fact, reflect similar gradients in species richness and abundance of lichens occurring on both oak and conifer species (Nash & Sigal 1999). In comparison with collections from the early 1900s when oxidant air pollution was essentially absent, 50 % fewer lichen species were found on conifers during four years of collecting and sampling in the mountains of Southern California (1976-1979, Sigal & Nash 1983).

Within populations of *Hypogymnia imshaugii* marked morphological changes were evident in randomly selected samples (increase in percentage of bleached samples and in percentage of convoluted samples), when compared to reference stands in the Cuyamaca Rancho State Park (CRSP, located 64 km east of San Diego). On hardwoods (*Quercus kelloggii*) 30 epiphytic species were found in the CRSP and 25 in SBM and it was concluded that oxidants appear to control the distribution of the most common black oak lichen, *Melanelia subolivacea*, but not the other lichen species. However, it is reasonable to postulate that these Californian lichens may actually have been responding to one or more alternative pollutants that occur in the Los Angeles region. For example during the field investigation period SO_2 concentrations were still high, the pollutant that was known to impair lichen cover significantly (Nash & Sigal 1999).

7.2.5.4.6 Insect communities

Oxidant air pollution may have indirect effects on the herbivory insects or pathogens through changes in the host, and direct and indirect effects on natural enemies of the insects or pathogen (see chapter 5.2 and 5.3).

As early as in the late sixties Cobb et al. (1968) and Cobb & Stark (1970) established a relationship between pollution injury of *P. ponderosa* and physiological properties associated with the susceptibility of the trees to bark beetles (*Dendroctonus brevicomis*). Trees showing severe injury symptoms were more frequently infested by *D. brevicomis* and *D. ponderosae* and vice versa at a plot with high levels of ozone, more than 80 % of trees which were killed by bark beetles were severely injured (Stark et al. 1968; Stark & Cobb 1969; Binkley et al. 1992). Studies on the productivity of the attacking beetles indicated that the number of trees a population of western pine beetle could kill is clearly related to the proportion of injured trees (Dahlsten et al. 1997; Pronos et al. 1999). In contrast, the distribution of the needleminer (*Coleotechnites* sp.) on *P. jeffreyi* could not be related to the oxidant air pollution (Luck 1976).

Regarding the herbivore communities Jones & Paine (2006) were able to show shifts in the community organisation by use of discriminant function analysis: For fern and oaks air pollution exposure mediated a shift from communities dominated by sucking insects to communities dominated by chewing insects, while changes in pine herbivore communities were less associated with the pollution gradient. However, the site factor of nitrogen pollution seemed to be dominant relative to the ozone exposure.

7.2.5.5 Conclusion

Research over several decades documented various impacts of high ozone levels on the mixed conifer stands in the SBM at the ecosystem-level. However, it must be mentioned that anthropogenic air pollution is not the only parameter affecting forest growth. The concurrence of drought, long-term reduction in precipitation, and high ozone has contributed to a period of growth decline in the San Bernardino Mountains. Different to controlled experiments within field observations other environmental factors became more important and reflect a general fact of air pollution research as there is no unique response of plants to oxidant stress. Instead, it is a set of characteristics of physiological changes that determines individual plant success or failure in the face of multiple stressors (Grulke 1999).

The ozone dose gradient was paralleled by a gradient of decreasing precipitation and air temperature (with increasing altitude). As a result, the most common conifer species forming the matrix of the forest mixtures shifted from *P. ponderosa* to *P. Jeffreyi* as precipitation and air temperature decreased. It was impossible to locate a site of analogous species mixtures, soil types, and climatic conditions, where air pollution was low or absent. It was necessary, therefore, to study the behaviour of organisms and ecosystem processes under various levels of ozone stress.

Since the 1990s the effects of multiple pollutants on carbon allocation and sequestration was brought into focus showing that nitrogen plays an important role, moreover, the gradient of N deposition was shown to be steeper than that of ozone (Fenn & Bytnerowicz 1993; Arbaugh et al. 1999; Bytnerowicz et al. 1999; Arbaugh et al. 2003). The high rates of N deposition at the western end of the gradient appear to compensate for, or indeed override, the adverse effects of ozone in this area (Temple et al. 2005). In addition, soil acidification, lower base saturation (Grulke et al. 1998) and higher annual precipitation (Arbaugh et al. 1999) were associated with the highest oxidant exposure. Therefore, more pollutant species should have been included into the causal analysis of air pollution effects in the San Bernardino Mountains (Miller et al. 1998b).

However, unlike the systematic study of ozone effects on injury and growth of overstory trees, no careful chronological sequence measurements of understory species frequency or density have been conducted along the air pollution gradient in the SBM (Temple et al. 2005). Shrub and herbaceous plant cover was measured once along the pollution gradient in 1970s (Taylor 1973), but these observations were not sufficient to establish a causal relationship between ambient ozone concentrations and changes in community structure or composition. Subsequent observations suggested that ozone may have had only minor direct effects on understory plant community composition in the SBM in comparison with other factors, such as habitat alteration, fire suppression, invasion by weedy plants, and N deposition (Temple 1999). The persistence of ozone-susceptible genotypes of various plant species in areas of prevailingly high ambient ozone concentrations implied that severe foliar ozone injury per se is not a sufficient selective pressure to alter significantly the genetic structure of these plant populations in the number of generations from the 1950s until the end of the century (Temple 1999).

Epiphytic lichen communities in the San Bernardino Mountains have been dramatically reduced both in species diversity and in numbers both historically and relative to comparable habitats with little air pollution (Nash and Sigal 1999). However, the role of ozone in this reduction, relative to other factors such as N deposition or other pollutants, has not been determined.

7.3 Field surveys in Europe

In the 1970s a new kind of forest damages was observed in Germany and other European countries. Since 1985 surveys of forest condition have been carried out annually in 35 European countries and were coordinated by the ICP Forests (International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests) under the Working Group on Effects of the Convention on Long-range Transboundary Air Pollution of UNECE. In 10 European countries participating in the UNECE program a more intensive assessment of ozone symptoms was initiated in 2000 (FIMCI 2003; Ferretti et al. 2007c; Paoletti 2007; http://www.icp-forests.org/Manual.htm).

Despite the prediction from the early 1980s, it is common knowledge that forest decline has been less dramatic (Lorenz 1995). However, the results of a 10-year monitoring across Europe showed that crown transparency increased with increasing levels of ozone. This increase was more significant in a mesophilic species like *Fagus sylvatica*, than in a xerotolerant species like *Quercus ilex* (Klap et al. 2000). In the timberline ecotone of the central European Alps and the Carpathian Mountains symptom expression on *Pinus cembra* was highly site-dependent showing ozone-like symptoms in the southern French Alps and in the Carpathians but not in the central European Alps (Wieser et al. 2006).

Although results of ICP Forests frequently indicated effects of ozone on leaves of forest trees and understory vegetation (Lorenz & Mues 2007) the unequivocal evidence for its causation by ozone has only been found in a few places in the Mediterranean Basin (Matyssek & Innes 1999; Lorenz & Mues 2007). Thus, a sub-program “Ozone at the intensive monitoring plots in South-Western European forests” (O_3SWE) was initiated, which refers to 83 sites in France, Italy, Luxembourg, Spain and Switzerland in order to focus on the south of Europe (Ferretti et al. 2007b). As a result, vegetation in humid areas such as the Italian Po Plane and the

Swiss Canton Ticino was more responsive than plant communities in countries like Spain or Greece (Lorenz et al. 2005; Paoletti 2007).

In could be summarised that despite the intensive and continuing survey and monitoring activities at different sites in Europe, the large data set of parameters describing the forest health status and foliar symptoms on more than 60 species during the last years information about its correlation with ozone is rather scare. Multivariate analysis confirmed that soil and site factors are important factors related to mean defoliation of *F. sylvatica* and a role of ozone was obvious only at extremely high exposure levels (Ferretti et al. 2007c).

7.3.1 Forest decline in Germany

In the early 1970s, *Abies alba* showed first symptoms of decline occurring almost simultaneously in the Black Forest and the Bavarian Forest (Blank 1985). Later in the 1970s and early 1980s, symptoms of decline became apparent on *Picea abies* (Krause et al. 1986; Prinz 1988). Based on growth chamber studies with *Picea abies* in the early 1980s it was suggested that ozone takes part in the forest dieback syndrome (Blank 1985; Krause et al. 1985; Prinz 1985; Krause et al. 1986; Rehfuess 1987). The prediction that a general forest decline would happen in Germany led to the development of integrated and ecosystem-oriented research programs in the FRG beginning in 1983 (Ulrich 1990) and in 1990 in the GDR (Wienhaus 2003). However, for *P. abies* grown in southwestern Germany there was no evidence of an acute ozone injury comparable to that of declining ponderosa pine is the San Bernardino Mountains in southern California (Huettl et al. 1990).

Schmieden & Wild (1995) critically reviewed the contributions of ozone to forest decline and stated that other stress factors specific for each site may lead to similar responses and chronic exposure to ambient ozone was thought to have changed the predisposition of trees, which increased sensitivity to abiotic factors such as frost, drought and high light intensity and hence may be one of the primary reasons for forest decline at central Europe.

Recently, in southern Germany minor ozone-like leaf injury symptoms were detected only at a few of the forest sites investigated (Baumgarten et al. 2009). However, according to the most common ozone thresholds in Europe, trees growing in the Bavarian forests appear to be at risk under the prevailing ozone regimes and climatic conditions and in terms of ozone uptake more attention should be directed to forest regions with non-limited water supply.

7.3.2 Mediterranean basin

In the Mediterranean basin, climatic features generally encourage the generation of high concentrations of ozone and due to sea-breeze inland transport high ozone concentrations have often been recorded in remote mountain regions with forested slopes (Bussotti & Ferretti 1998; Bussotti & Gerosa 2002). Therefore, in southern Europe the areas most impacted by ozone are densely-populated regions, often near the coasts. This is especially the case in Athens and its surroundings, in parts of the coast of eastern Spain, and the Po valley in north Italy. As a result, *Pinus halepensis*, which is the most widespread species of pine in the Mediterranean region, was found to be of poor condition in Israel (Naveh et al. 1980), Greece (Velissariou et al. 1992; Gimeno et al. 1995) and Spain (Sanz et al. 1999; 2000), where leaf injury assessment correlated with the penetration of pollutants transported by the sea-breeze into coastal valleys of Castellon.

Results of data recording suggest that Italy may be considered as a hot-spot for ozone and can be regarded as representative of ozone impacts on Mediterranean vegetation (Paoletti 2007). Estimated AOT40 values ranged between 4000 and 26000 ppb h^{-1} (1996-2000, June-September, Gerosa & Anfodillo 2003; Gerosa et al. 2003) and indicated a frequent exceeding of the critical level (Ferretti et al. 2003b; Ferretti et al. 2005). Areas with the highest ozone concentration levels are located in Central and Southern Italy and in the Alpine region (Mangoni & Buffoni 2005).

In 1995, an National Integrated Programme for Forest Ecosystem Monitoring (Italian acronym: CONECOFOR, CONtrolli ECOsistemi FORestali[6] was initiated within the framework of the intensive forest monitoring programme carried out under the auspices of the United Nations Economic Commission for Europe (UNECE, Ferretti et al. 2003b). Effects of the impact of high ozone episodes on vegetation have been surveyed by means of the assessment of visible ozone-like symptoms, crown transparency and basal area increment of dominant trees (Bussotti et al. 2003a). Ozone-like visible foliar symptoms were recorded at 47 % of the common monitoring sites in 2001 and 38 % in 2002. The list of all species is given in Table 21. However, there was no relationship between estimated mean AOT40 and frequency of symptomatic sites and frequency of species with symptoms (Bussotti et al. 2003a; Ferretti et al. 2007c; Ferretti et al. 2007a), as other environmental factors such as depth and moisture of the soil are changing with leaf injury frequency (Bussotti et al. 2003b).

Due to the incorporation of additional investigations related to biodiversity data about forest structure and vascular plant diversity covering a time period of about 10 years are available (Ferretti et al. 2006b). For beech plots, correlation studies identified N to play a significant role in predicting species richness (Ferretti et al. 2006a).

In conclusion, field evidence of direct effects of ozone on Italian forests remained controversial. Due to the high variability of the physical (altitude, slope, exposure, etc.) features and vegetation (species assemblage, tree age, forest structure), the comparability among the plots was found to be very weak (Bussotti et al. 2003b). In fact, up to 90 % of the data variance was explained by site factors, moreover, significant relationships between ozone exposure and effects often failed. For example, symptoms on beech were found at one site only and this one was not the site with the highest AOT, assuming that other ecological conditions may favour the uptake of ozone (Bussotti et al. 2003a). Paoletti (2007) suggested to explain this fact by an adaptation of Mediterranean forests to oxidative stress including ozone.

---

[6] http://www.idrolab.ise.cnr.it/index.php?option=com_content&view=article&id=56&Itemid=56&lang=en)

Table 21: Species exhibiting ozone-specific and ozone-like symptoms recorded during the 2001- 2003 survey in Italy.

shrubs and trees	reference	herbaceous plants	reference
Acer platanoides	Bussotti et al. (2003a)	*Alchemilla vulgaris*	Bussotti et al. (2003a)
Acer pseudoplatanus	Bussotti et al. (2003a, 2006)	*Arunus dioicus*	Bussotti et al. (2003a)
Alianthus altissima	Bussotti et al. (2003a)	*Astrantia major*	Bussotti et al. (2003a, 2006)
Carpinus betulus	Bussotti et al. (2003a)	*Atropa belladonna*	Bussotti et al. (2003a)
Clematis vitalba	Bussotti et al. (2003a, 2006)	*Beta vulagris*	Bussotti et al. (2003a)
Cornus mas	Bussotti et al. (2003a)	*Cardamine heptaphylla*	Bussotti et al. (2003a)
Corylus avellana	Bussotti et al. (2003a)	*Centaurea niger*	Bussotti et al. (2003a)
Crataegus monogyna	Bussotti et al. (2003a)	*Centaurea nigrescens*	Bussotti et al. (2003a)
Fagus sylvatica	Bussotti et al. (2003a, 2006)	*Centaurea sp. pl.*	Bussotti et al. (2006)
Fraxinus excelsior	Bussotti et al. (2003a, 2006)	*Cyclamen sp. pl.*	Bussotti et al. (2006)
Fraxinus ornus	Bussotti et al. (2003a)	*Eupatorium cannabium*	Bussotti et al. (2003a)
Laburnum alpinum	Bussotti et al. (2003a, 2006)	*Euphorbia dulcis*	Bussotti et al. (2003a, 2006)
Lonicera caprifolium	Bussotti et al. (2003a)	*Gentiana asclepiadea*	Bussotti et al. (2006)
Ostrya carpinifolia	Bussotti et al. (2003a)	*Geranium nodosum*	Bussotti et al. (2003a)
Parthenocissus	Bussotti et al. (2003a)	*Globularia nudicaulis*	Bussotti et al. (2006)
Picea abies	Bussotti et al. (2003a)	*Helleborus niger*	Bussotti et al. (2003a, 2006)
Pinus halepensis	Bussotti et al. (2003a)	*Heracleum sphondylium*	Bussotti et al. (2003a)
Prunus avium	Bussotti et al. (2003a)	*Lamium spp..*	Bussotti et al. (2003a)
Prunus spinosa	Bussotti et al. (2003a)	*Lapsana communis*	Bussotti et al. (2003a)
Robinia pseudacacia	Bussotti et al. (2003a)	*Mercurialis perennis*	Bussotti et al. (2003a)
Robinia	Bussotti et al. (2006)	*Mycelis muralis*	Bussotti et al. (2003a)
Rosa canina	Bussotti et al. (2003a)	*Pastinaca sativa*	Bussotti et al. (2006)
Rubia peregrina	Bussotti et al. (2006)	*Polygonatum sp.*	Bussotti et al. (2006)
Rubus idaeus	Bussotti et al. (2003a)	*Rumex alpinum*	Bussotti et al. (2003a)
Rubus sp. pl.	Bussotti et al. (2003a, 2006)	*Rumex sanguineus*	Bussotti et al. (2003a)
Salix alba	Bussotti et al. (2003a)	*Salvia glutinosa*	Bussotti et al. (2003a)
Sambucus ebulus	Bussotti et al. (2003a)	*Scrophularia nodosa*	Bussotti et al. (2003a)
Sambucus racemosa	Bussotti et al. (2003a)	*Stachys sp. pl.*	Bussotti et al. (2006)
Sorbus aucuparia	Bussotti et al. (2003a)	*Thalictrum minus*	Bussotti et al. (2003a)
Tilia cordata	Bussotti et al. (2003a)	*Urtica dioica*	Bussotti et al. (2003a)
Ulmus glabra	Bussotti et al. (2003a)	*Valeriana officinalis*	Bussotti et al. (2003a)
Ulmus minor	Bussotti et al. (2003a)	*Veronica urticifolia*	Bussotti et al. (2003a)
Vaccinium myrtillum	Bussotti et al. (2006)		
Viburnum lantana	Bussotti et al. (2003a, 2006)		
Vitis vinifera	Bussotti et al. (2003a, 2006)		

7.3.3 The Carpathian Mountains Network Study

7.3.3.1 Site description

The Carpathian Mountains form the second high mountain range in Europe after the Alps. With a total length of about 1,500 km it covers about 209,000 km² (Badea et al. 2011) and enclose some of the most beautiful areas in Europe (Bytnerowicz et al. 2003). Its largest portion (55.5 %) is located in Romania followed by Poland, Slovakia, Ukraine, Hungary, and the Czech Republic (Bytnerowicz et al. 2003). With the exception of the Tatras region the touristic utilization of these mountains is rather low.

It is incontestable that the Carpathian Mountains represent a natural treasure of great beauty and ecological value (Badea et al. 2011), an unique reservoir of many endemic, rare, and unusual plant and animal species (Szaro et al. 2002; Bytnerowicz et al. 2003), and for biodiversity (Grodzinska et al. 2004). In 1998, phyto-sociological records revealed a total number of vascular plant species of 269, within single plots this number range from 20 to 91 species in individual records (Grodzinska et al. 2002; Grodzinska et al. 2004).

Because of its importance for preservation of biodiversity, several national parks have been established in order to protect the rich and varied vegetation and remnants of original natural ecosystems (Bytnerowicz et al. 2003; Badea et al. 2011). The Retezat Mountains in the Southern Carpathian Mountains, Romania, which has been declared a national park already in 1935, represents exceptional biological value for the entire Carpathian range. The rich flora of the alpine area, the presence of 61 different herbal and wood associations, and the high diversity of mosses and of lichen associations describes this high value from the view of biodiversity (Bytnerowicz et al. 2001). Across the entire area over 1100 plant species have been identified (Badea et al. 2011), the main tree species are *Picea abies* (81 %), *Fagus sylvatica* (12 %), *Abies alba* (4 %) and *Betula pendula* (2 %, Bytnerowicz et al. 2001). *Acer pseudoplatanus, Pinus sylvestris,* and *Sorbus aucuparia* are secondary species (Badea et al. 2011). More than 30 % of forests in the Retezat Mountains are natural (Bytnerowicz et al. 2001). Dendrometric parameters of trees demonstrate higher diversity in European beech and mixed stands than in Norway spruce pure stands (Badea et al. 2011). Within the area of the Tatra Mountains, however, 50 % of forests have natural or semi-natural structure (Bytnerowicz et al. 2003). On the other hand, intensive silviculture practiced at the end of the 19th and the beginning of the 20th centuries resulted in secondary, monospecific stands concomitant with reduced biodiversity of ecosystems (Grodzki et al. 2002).

7.3.3.2 The monitoring network

In recent times, evidence was growing to suggest that long-range transport of ozone from Western Europe and the generation of ozone from local and regional precursors may impact Central and Eastern Europe and in this way may pose a threat on the ecosystems in the Carpathian Mountains. So, the national parks within the Carpathian Mountains gained attention for European research in the context of climate change and air pollution effects (Badea et al. 2011). An international cooperative project “Evaluation of Ozone Air Pollution and Its Phytotoxic Potential in the Carpathian Forests” was performed in the late 1990s. Data on concentrations of ozone, SO_2, and NO_2 monitored at 30 plots showed that in many forest locations of large parts of the Carpathian Mountains levels of ozone were elevated and potentially phytotoxic to forest vegetation. 26 permanent study sites were established in the vicinity of the ozone monitoring sites to describe forest vegetation and health status of selected forest stands including phyto-sociological records (Grodzinska et al. 2004).

The first results led to the establishment of two International Long-Term Ecological Studies (ILTER) on effects of air pollution on forests and other ecosystems in the **Retezat Mountains**, Southern Carpathians, Romania and in the **Tatra Mountains**, Western Carpathians on the Polish-Slovak border leading to a multinational and multidisciplinary network (Bytnerowicz et al. 2001; Bytnerowicz et al. 2003; Bytnerowicz et al. 2004b). In the Retezat Mountains, the primary research objective was to evaluate how air pollution may affect forest health and biodiversity. A monitoring network in the Retezat Mountains consists of 10 permanent plots established in June 2000. At each of the research sites, species composition of the understory vegetation should be described each year, tree inventory and crown conditions should be evaluated (Bytnerowicz et al. 2001; Badea et al. 2002; Szaro et al. 2002; Bytnerowicz et al. 2003).

7.3.3.3 Exposure to air pollution

The Central European countries, such as Czech Republic, Poland, Romania, Slovakia and Ukraine, and consequently the Carpathian Mountains are characterised by a long history of pollutant impacts. Beginning in the middle of the 20th century, long-range transport of pollutants from various European industrial areas resulted in the high deposition of a variety of phytotoxic air pollutants, including heavy metals, nitrogen oxides and nitrates, sulphur dioxide and sulphates (Grodzińska & Szarek-Łukaszewska 1997; Manning et al. 2002; Grodzinska et al. 2004). As a result of this industrial pollution scenario, symptoms of declining tree health have been observed in the majority of central European forest with an extensive decline of the Carpathian forests (Godzik & Sienkiewicz 1990). Since the late 1980s, several efforts in reducing the levels of industrial pollutants in Central Europe had become successful and as a consequence adverse impacts on forest condition have been diminished. Simultaneously, rapid increase of combustion from industrialization, urbanization and vehicular traffic resulted in release of higher levels of hydrocarbons and oxides of nitrogen, which in turn resulted in formation of ozone above background level (Bytnerowicz et al. 2001; Manning et al. 2002; Grodzinska et al. 2004, see Table 22).

Table 22: Characteristics of ozone pollution in the Carpathian Mountains, Central Europe. avg. = average, seas. = seasonal.

time period	site	index of ozone exposure			reference
		avg. peak	seas. mean	2-wk mean	
1995	Ukrainian Carpathians			27-52 ppb	Blum et al. (1997); Blum et al. (1998)
1997	Retezat			19-31 ppb	Bytnerowicz et al. (2001)
	Stana de Vale			48-59 ppb	Bytnerowicz et al. (2001)
1994 - 1999	Czech Republic	70-80 ppb	14-66 ppb		Moravcik et al. (2002)
1997 - 1999	Bucegi Romania		39-42 ppb		Silaghi & Badea (2012)
2006 - 2008	Bucegi Romania		43-47 ppb		Silaghi & Badea (2012)
2009	Bucegi Romania		40 ppb		Silaghi & Badea (2012)

However, different to other European countries, Romania and Poland showed considerably high SO_2 emissions in the 1990s (Cerny et al. 2002; Muzika et al. 2002) leading to the fact that ozone represents only one component of oxidative air pollution differing in time, space and composition. For example the Retezat Mountains have been characterised by low levels of ozone, SO_2, NO_2, and N deposition, while elevated levels of ozone as well as high deposition of atmospheric S and N have been monitored in the Tatra Mountains (Bytnerowicz et al. 2003).

At the end of the 20th century levels of pollutants in Slovakia, Poland and the Czech Republic were classified to be still among the highest (Muzika et al. 2002). For ozone passive sampler monitoring showed a high spatial diversity of concentrations with the highest ozone concentrations being expected especially in the western part of the Carpathian Mountains (Szaro et al. 2002). Reviewing all ozone monitoring data available for the forested areas of the Central and Eastern European Mountains for the period of 1994 to 2000, Bytnerowicz et al. (2004c) ascertained low European background concentration (summer season means 30 ppb) for some areas in Romania, Poland and Czech Republic (see Table 22). On the contrary, seasonal means of about 50 ppb were found to occur especially in the western part of the range (Slovakia, the Czech Republic and Poland) and some of the Eastern and Southern Carpathians. The highest ozone concentrations in the Western Carpathian Mountains reached 80 to 100 ppb during the summer season (Bytnerowicz et al. 2003). Referring to the effect of elevation an increase of ozone concentration with altitude was noticed, but the correlation was not statistically significant (Badea et al. 2011). During the seasons 2006 to 2009 mean ozone concentration were at least as high as in the 1997 to 1999 period, when compared at four intensive forest monitoring plots (Silaghi & Badea 2012). The intensive monitoring work clearly indicated that parts of the Carpathian Mountains experienced ozone exposures above the levels recommended for protection of forest and natural vegetation. However, ozone effects may not be easy to detect due to a presence of other pollutants that also may be toxic to plants, especially SO_2 (Bytnerowicz et al. 2004c; Bytnerowicz et al. 2004a).

7.3.3.4 Ozone effects

The multinational and multidisciplinary assessment network program of the Carpathian Mountains targets on several aspects of ecosystem integrity. Thus, forest health monitoring including understory plant cover, dendrochronological measurements, estimation of tree mortality, and with special regard to biodiversity phyto-sociological and genetic evaluation had been done and are still going on.

7.3.3.4.1 Forest health

The results from the transnational networks showed that the Carpathian forests are slightly more damaged than the average for the entire Europe (Badea et al. 2004). Damage on Norway spruce (*Picea abies*) and silver fir (*Abies alba*) were the highest and pines (primarily *Pinus sylvestris*) were the least affected of the conifers. For the Slovakia Oszlányi (1997) reported on average defoliation rates of up to 35 % for coniferous species and up to 27 for broadleaved species during the period of 1987 to 1994. For Poland average defoliation ranged between 30 and 40 % for *P. abies* during the late 1990s (Purdon et al. 2004). However, the degree of crown damage varied greatly between the investigated sites. Trees from the western part of the Carpathians show the greatest degree of defoliation. The decrease in damage from west to east corresponded with the levels of ozone monitored in these areas (Grodzinska et al. 2002; Grodzinska et al. 2004) and forest decline was more pronounced for the Tatra Mountains (Bytnerowicz et al. 2003). The ambient ozone (described as seasonal mean concentrations among locations) had no significant influence on forest health status in Retezat and Bucegi Mts (Badea et al. 2011), where ozone concentrations were rather low.

A dramatic forest decline due to the bark beetle outbreak, which occurs in the Norway spruce stands in the Western Beskidy (southern Poland) since 2003, was observed after severe physiological drought during winter time (Grodzki 2007). In 2003 and 2006 the bark beetle occurrence level assessed as high and catastrophic was recorded on 40 % and 59 % of the area, respectively. The range of *Armillaria* root disease and bark beetle outbreak increased towards higher altitudes, including the zone above 1,000 m a.s.l. The wind damage in 2004 and 2007, and high temperatures in the summer 2006, further stimulated the increase in bark beetle population level (Grodzki 2007). Significantly higher captures of *Ips typographus* and higher infestation densities were recorded in the plots with high ozone (Grodzki et al 2002; 2004).

7.3.3.4.2 Tree mortality and forest productivity

The volume of sanitary cuttings representing an evidence of tree mortality was analysed during the period 1995 - 2000. It was apparent that the volume of sanitary cuttings was higher in stands ranked as exposed to higher levels of ozone. Although in the Tatra Mountains bark beetles seemed to be the immediate reason of large-scale forest decline a combination of multiple factors including elevated ozone and high sulphur and nitrogen depositions is thought be the cause of these ecological problems (Bytnerowicz et al. 2003).

On 17 sites, divided into high polluted or low polluted plots, dendrochronological studies were done for both *Fagus sylvatica* and *Picea abies* in order to calculate the basal area increment growth (BAI) for the 1955 to 1999 period. The results indicated that at high polluted sites the BAI has declined approximately 50 % and 20 %, respectively, over the last 45 years of the 20th century. There is a strong divergence between two pollution regimes: after 1980 at high pollution sites BAI remains unchanged while at low pollution sites increased growth of both tree species was measured. For both species, all growth variables did not correlate with the ozone level alone, but significantly and strongly correlated with a pollution variable that combines mean levels of ozone, SO_2 and NO_2, reflecting the high sulphur emissions in Romania and Poland (Muzika et al. 2002; Muzika et al. 2004).

Table 23: Species exhibiting ozone-specific and ozone-like symptoms recorded in the Carpathian Mountains, Central Europe.

shrubs and trees	reference	herbaceous plants	reference
Alnus incana	Manning et al. (2002)	*Alchemilla sp.*	Manning et al. (2002)
Clematis hyb.	Blum et al. (1997)	*Astrantia major*	Manning et al. (2002)
Clematis vita-alba	Manning et al. (2002)	*Centaurea jacea*	Godzik & Grodzinska (2002)
Cornus sanguinea	Manning et al. (2002)	*Centaurea nigra*	Manning et al. (2002)
Corylus avellana	Blum et al. (1997); Manning et al. (2002); Godzik & Grodzinska (2002)	*Centaurea scabiosa*	Manning et al. (2002)
Humulus lupulus	Blum et al. (1997); Manning et al. (2002)	*Chaerophyllum aromaticum*	Manning et al. (2002)
Lonicera nigra	Manning et al. (2002)	*Gentiana asclepiadea*	Manning et al. (2002); Godzik & Grodzinska (2002)
Parthenocissus quinquefolia	Manning et al. (2002)	*Geranium palustre*	Manning et al. (2002)
Pinus cembra	Manning et al. (2002); Godzik & Grodzinska (2002)	*Impatiens parviflora*	Manning et al. (2002); Godzik & Grodzinska (2002)
Rubus hirtus	Blum et al. (1997)	*Lapsana communis*	Manning et al. (2002)
Salix caprea	Manning et al. (2002)	*Ranunculus lanuginosus*	Godzik & Grodzinska (2002)
Sambucus	Blum et al. (1997); Manning	*Ranunculus repens*	Godzik & Grodzinska (2002)

shrubs and trees	reference	herbaceous plants	reference
racemosa	et al. (2002); Godzik & Grodzinska (2002)		
Sorbus aucuparia	Manning et al. (2002); Godzik & Grodzinska (2002)	*Senecio subalpinus*	Godzik & Grodzinska (2002)
Ulmus excelsior	Manning et al. (2002)	*Stachys officinalis*	Manning et al. (2002)
Ulmus laevis	Manning et al. (2002)	*Thymus alpestris*	Manning et al. (2002)
Ulmus montana	Manning et al. (2002)	*Vincetoxicum officinalis*	Manning et al. (2002)
Vaccinium myrtillus	Manning et al. (2002); Godzik & Grodzinska (2002)		
Viburnum opulus	Manning et al. (2002)		
Viburnum sp.	Manning et al. (2002)		
Vicentoxicum sp.	Blum et al. (1997)		

7.3.3.4.3 Effects on biodiversity

When approaching aspects of biodiversity in context with air pollution differential response or tolerance of single species or populations to the stressors remains one main parameter to refer to potential selection events. Thus even in the Carpathian Mountains detections of ozone sensitive plant species and populations was one topic. In summary, for 20 woody and 16 herbaceous plant species the occurrence of ozone-specific or ozone-like visible symptoms of leaf injury has been documented in the literature (see Table 23).

At two sites (Retezat and Bucegi Mts) phyto-sociological evaluation have been carried out by Badea et al. (2011) each in 2000 and 2009. Their results showed that there was no evidence of a rapid and furthermore no significant reduction of biodiversity.

7.3.4 Lithuania

As already shown for the Carpathian Mountains the ecosystems in the North-East of Europe are still subjected to the impact of SO_2 and NO_2. In Lithuania, within the framework of the 'The Integrated Monitoring Programme' long-term investigations have been undertaken to estimate the contribution of ozone to the integrated impact of acid deposition and the amount of precipitation on trees' health and growth). Defoliation of both conifers and deciduous trees correlated well with the acidity of precipitation and the concentrations of SO_2 and NO_2 (Ozolincius et al. 2005; Augustaitis et al. 2007a). In contrast, the proportion of healthy trees seemed to be related more to the average temperature and ozone (Ozolincius et al. 2005). By means of multiple regression analysis for *Pinus sylvestris* it was shown that the contribution of peak ozone concentrations to the integrated impact of defoliation and on the increment residuals was most significant (Augustaitis et al. 2007b; Augustaitis et al. 2007a). Mean annual ozone concentrations did not affect pine (*P. sylvestris*) defoliation (Augustaitis 2011), whereas peak concentrations of ambient ozone might have a negative impact on pine tree crown defoliation and stem growth reduction under field conditions in central and north-eastern Europe (Augustaitis et al. 2007b; Augustaitis & Bytnerowicz 2008). Thus, results of monitoring program from more than 15 years in Lithuania revealed that the key factor contributing to increment residual changes could have been peak ozone concentrations while SO_2 reinforced the ozone effect on stem increment (Augustaitis et al. 2007b; Augustaitis & Bytnerowicz 2008; Augustaitis 2010).

Table 24: Species exhibiting ozone-specific and ozone-like symptoms recorded in Lithuania.

shrubs and trees	reference
Pinus sylvestris	Augustaitis et al. (2007a), Augustaitis et al. (2007b) Augustaitis (2011)
Fagus sylvatica	Augustaitis et al. (2012)
Rubus idaeus	Ozolincius & Serafinaviciute (2003)
Alnus incana	Ozolincius & Serafinaviciute (2003)
Salix caprea	Ozolincius & Serafinaviciute (2003)
Frangula alnus	Ozolincius & Serafinaviciute (2003)
Fraxinus excelsior	Girgzdiene et al. (2009), Ozolincius et al. (2005)

There is evidence that present relatively low levels of tropospheric ozone in Eastern Europe are high enough to have a negative effect on vegetation. Out of a list of 46 Lithuanian species sensitive to ozone, on four tree and shrub species ozone-specific symptoms have been found (Ozolincius & Serafinaviciute 2003) and more visible ozone injuries were found in the eastern part of Lithuania, where higher tropospheric ozone concentrations were recorded (Table 24).

Ozone negatively influenced the response of growth of *Fagus sylvatica* to climatic conditions which are critical for growth outside their north-eastern distribution range (Augustaitis et al. 2012). During the 15 years of intensive monitoring the condition of *Fraxinus* excelsior declined considerably (Girgzdiene et al. 2009). The mean defoliation increased 2–3 times and reached 35 %–40 %, which was strongly correlated with the ozone exposure (Ozolincius et al. 2005; Girgzdiene et al. 2009). After investigating the long-term effect of background air pollution on the condition of the main tree species in Lithuanian forests, *F. excelsior* appeared to be one of the most sensitive tree species. In conclusion, there seemed to be a difference between life strategy because it was suggested that deciduous species are more sensitive to ozone and conifers were found to be more susceptible to SO_2 (Ozolincius et al. 2005).

Further investigations of Augustaitis et al. (2007c) indicated that there is evidence of ozone effects on diversity of soil arthropods, and in some cases, small mammals and stream invertebrates. The strongest relationships have been established between peak ozone concentrations and Oribatidae and Acaridae.

7.4 Conclusion

At first view, there is a large number of references which report on studies examining the influence of ozone within field surveys of ecosystem condition and composition. Nevertheless, on closer examination significance of a causal relationship to ozone exposure proved to be poor. Field observation assessments based upon either temporal or spatial variations in ozone exposure levels and both kinds of variations are shown to be accompanied by variations of further environmental parameters such as N deposition, soil moisture, soil texture or altitude. Multivariate methods of statistical analysis have been demonstrated to estimate the part of ozone in contributing to observed effects, which in turn may be interpreted only in relation to these co-factors. Detection of ozone-specific symptoms of leaf injury seem to be one tool, which is worldwide established and suitable to afford a significant cause-response relationship and therefore implemented into the level II observations of ICP forests. However, the absence of symptomatic plants may be reasoned by either the absence of phytotoxic levels of ozone or the absence of sensitive species genotypes as a result of adaptation to previous high exposure scenarios.

In terms of growth and timber production dendrochronological investigations had been applied to estimate growth reductions caused by ozone in California (Miller & Arbaugh, 2000), Sweden

(Karlsson et al. 2006), and to a certain extent in the Carpathian Mountains (Muzika et al. 2002; Muzika et al. 2004).

In California, a change in community composition and species diversity of understory vegetation in mixed conifer stands during 30 years has been observed, which was shown to be attributed to high ozone exposures (Allen et al. 2007). Because of the short time period phyto-sociological surveys from the Carpathian Mountains did not bring out results until now (Grodzinska et al. 2004).

7.5 References

Allen, E. B., Temple, P. J., Bytnerowicz, A., Arbaugh, M. J., Sirulnik, A. G. & Rao, L. E. (2007): Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution. Thescientificworldjournal 7, 247-263.

Alonso, R., Bytnerowicz, A. & Arbaugh, M. (2002): Vertical distribution of ozone and nitrogenous pollutants in an air quality Class I area, the San Gorgonio Wilderness, Southern California. Thescientificworldjournal 2, 10-26.

Arbaugh, M., Bytnerowicz, A., Grulke, N., Fenn, M., Poth, M., Temple, P. & Miller, P. (2003): Photochemical smog effects in mixed conifer forests along a natural gradient of ozone and nitrogen deposition in the San Bernardino Mountains. Environment International 29, 401-406.

Arbaugh, M. J., Peterson, D. L. & Miller, P. R. (1999): Air pollution effects on growth of Ponderosa pine, Jeffrey pine, and bigcone Douglas-fir. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. M. J. R. Miller), pp. 179-207.

Arbaugh, M. J., Miller, P. R., Carroll, J. J., Takemoto, B. & Procter, T. (1998): Relationships of ozone exposure to pine injury in the Sierra Nevada and San Bernardino Mountains of California, USA. Environmental Pollution 101, 291-301.

Augustaitis, A. (2010): Air Pollution, Their Integrated Impact on Forest Condition Under Changing Climate. In Air Pollution (ed. by V. Villanyi). DOI: 10.5772/10046.

Augustaitis, A. (2011): The changes in pine forest condition under the global pressures in Lithuania. Transilvania University Press, Brasov, Romania. In Proceedings of the Biennial International Symposium, Forest and Sustainable Development, Brasov, Romania, 15-16th October 2010, Transilvania University Press, Brasov, Romania, pp. 17-22.

Augustaitis, A. & Bytnerowicz, A. (2008): Contribution of ambient ozone to Scots pine defoliation and reduced growth in the Central European forests: A Lithuanian case study. Environmental Pollution 155, 436-445.

Augustaitis, A., Augustaitiene, I., Kliucius, A., Girgzdiene, R. & Sopauskiene, D. (2007a): Contribution of ambient ozone to changes in scots pine defoliation. Step II of Lithuanian studies. Thescientificworldjournal 7, 47-57.

Augustaitis, A., Jasineviciene, D., Girgzdiene, R., Kliucius, A. & Marozas, V. (2012): Sensitivity of Beech Trees to Global Environmental Changes at Most North-Eastern Latitude of Their Occurrence in Europe. Thescientificworldjournal, DOIi: 10.1100/2012/743926

Augustaitis, A., Augustaitiene, I., Cinga, G., Mazeika, J., Deltuvas, R., Juknys, R. & Vitas, A. (2007b): Did the ambient ozone affect stem increment of scots pines (Pinus sylvestris L.) on territories under regional pollution load? Step III of Lithuanian studies. Thescientificworldjournal 7, 58-66.

Augustaitis, A., Augustaitiene, I., Kliucius, A., Mozgeris, G., Pivoras, G., Girgzdiene, R., Arbaciauskas, K., Eitminaviciute, I. & Mazeikyte, R. (2007c): Trend in ambient ozone and an attempt to detect its effect on biota in forest ecosystem. Step I of Lithuanian studies. Thescientificworldjournal 7, 37-46.

Badea, O., Popescu, F., Bytnerowicz, A., Musselman, R., Cenusa, R., Barbu, I., Gancz, V. & Tanase, M. (2002): Long term effects of air pollution on selected forest ecosystems in the Carpathian mountains (Retezat National Park, Romania).

Badea, O., Tanase, M., Georgeta, J., Anisoara, L., Peiov, A., Uhlirova, H., Pajtik, J., Wawrzoniak, J. & Shparyk, Y. (2004): Forest health status in the Carpahian Mountains over the period 1997-2001. Environmental Pollution 130, 93-98.

Badea, O., Neagu, S., Bytnerowicz, A., Silaghi, D., Barbu, I., Iacoban, C., Popescu, F., Andrei, M., Preda, E., Iacob, C., Dumitru, I., Iuncu, H., Vezeanu, C. & Huber, V. (2011): Long-term monitoring of air pollution effects on selected forest ecosystems in the Bucegi-Piatra Craiului and Retezat Mountains, southern Carpathians (Romania). Iforest-Biogeosciences and Forestry 4, 49-60.

Baumgarten, M., Huber, C., Bueker, P., Emberson, L., Dietrich, H.-P., Nunn, A. J., Heerdt, C., Beudert, B. & Matyssek, R. (2009): Are Bavarian Forests (southern Germany) at risk from ground-level ozone? Assessment using exposure and flux based ozone indices. Environmental Pollution 157, 2091-2107.

Benoit, L. F., Skelly, J. M., Moore, L. D. & Dochinger, L. S. (1982): Radial growth reductions of Pinus trobus L. correlated with foliar ozone sensitivity as an indicator of ozone-induced losses in eastern forests. Canadian Journal of Forest Research-

12, 673-678.

Binkley, D., Droessler, T. D. & Miller, J. (1992): Pollution Impacts at the Stand and Ecosystem Level. In: The response of western forests to air pollution. (ed. by R. K. B. D. B. M. Olson), pp. 235-257.

Blank, L. W. (1985): A new type of forest decline in Germany. Nature 314, 311-314.

Blum, O., Bytnerowicz, A., Manning, W. & Popovicheva, L. (1997): Ambient tropospheric ozone in the Ukrainian Carpathian Mountains and Kiev region: Detection with passive samplers and bioindicator plants. Environmental Pollution 98, 299-304.

Blum, O., Bytnerowicz, A., Manning, W. & Popovicheva, L. (1998): Ozone air pollution in the Ukrainian Carpathian Mountains and Kiev region. General Technical Report - Pacific Southwest Research Station, USDA Forest Service, 45-50.

Bussotti, F. & Ferretti, M. (1998): Air pollution, forest condition and forest decline in Southern Europe: an overview. Environmental Pollution 101, 49-65.

Bussotti, F. & Gerosa, G. (2002): Are the Mediterranean forests in Southern Europe threatened from ozone? Journal of Mediterranean Ecology 3, 23-34.

Bussotti, F., Cozzi, A. & Bettini, D. (2003a): Ozone-like visible foliar symptoms at the permanent monitoring plots of the CONECOFOR programme in Italy. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 99-106.

Bussotti, F., Cozzi, A. & Ferretti, M. (2006): Field surveys of ozone symptoms on spontaneous vegetation. Limitations and potentialities of the European programme. Environmental Monitoring and Assessment 115, 335-348.

Bussotti, F., Mazzali, C., Cozzi, A., Ferretti, M., Gravano, E., Gerosa, G. & Ballarin-Denti, A. (2003b): Ozone injury symptoms on vegetation in an Alpine valley, North Italy. In: Air Pollution, Global Change and Forests in the New Millennium (ed. by D. F. Karnosky, K. E. Percy et al.), pp. 269-276.

Bussotti, F., Schaub, M., Cozzi, A., Krauchi, N., Ferretti, M., Novak, K. & Skelly, J. M. (2003c): Assessment of ozone visible symptoms in the field: perspectives of quality control. Environmental Pollution 125, 81-89.

Bytnerowicz, A., Musselman, R. & Szaro, R. (2004a): Effects of air pollution on the Central and Eastern European mountain forests - Introduction. Environmental Pollution 130, 1-3.

Bytnerowicz, A., Fenn, M. E., Miller, P. R. & Arbaugh, M. J. (1999): Wet and dry pollutant deposition to the mixed conifer forest. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. M. J. R. Miller), pp. 235-269.

Bytnerowicz, A., Badea, O., Fleischer, P. & Grodzinska, K. (2004b): Science, land management and policy in international studies on the effects of air pollution on carpathian forest ecosystems. Scandinavian Journal of Forest Research 19, 129-137.

Bytnerowicz, A., Arbaugh, M., Schilling, S., Fraczek, W. & Alexander, D. (2008): Ozone distribution and phytotoxic potential in mixed conifer forests of the San Bernardino Mountains, Southern California. Environmental Pollution 155, 398-408.

Bytnerowicz, A., Arbaugh, M., Schilling, S., Fraczek, W., Alexander, D. & Dawson, P. J. (2007): Air pollution distribution patterns in the San Bernardino Mountains of southern California: a 40-year perspective. Thescientificworldjournal 7, 98-109.

Bytnerowicz, A., Godzik, B., Grodzinska, K., Fraczek, W., Musselman, R., Manning, W., Badea, O., Popescu, F. & Fleischer, P. (2004c): Ambient ozone in forests of the Central and Eastern European mountains. Environmental Pollution 130, 5-16.

Bytnerowicz, A., Badea, O., Popescu, F., Barbu, I., Postelicu, D., Vasile, C., Musselman, R., Manning, W., Stanciu, E. & Tamas, S. (2001): Long-term ecological research and air pollution impacts in the Retezat Mountains, Romania. Ekologia-Bratislava 20, 34-42.

Bytnerowicz, A., Badea, O., Barbu, I., Fleischer, P., Fraczek, W., Gancz, V., Godzik, B., Grodzinska, K., Grodzki, W., Karnosky, D., Koren, M., Krywult, M., Krzan, Z., Longauer, R., Mankovska, B., Manning, W. J., McManus, M., Musselman, R. C., Novotny, J., Popescu, F., Postelnicu, D., Prus-Glowacki, W., Skawinski, P., Skiba, S., Szaro, R., Tamas, S. & Vasile, C. (2003): New international long-term ecological research on air pollution effects on the Carpathian Mountain forests, Central Europe. Environment International 29, 367-376.

Cerny, M., Bytnerowicz, A., Moravcik, P., Musselman, R. & Hola, S. (2002): Ozone distribution and effects on plants in the Jizerske mountains, the Czech Republic. In: Effects of air pollution on forest health and biodiversity in forests of the Carpathian Mountains. Proceedings of the NATO Advanced Research Workshop, Stara Lesna, Slovakia, 22-26 May 2002 (ed. by R. C. Szaro, A. Bytnerowicz &J. Oszlanyi), pp. 285-295.

Chappelka, A., Somers, G. & Renfro, J. (1999a): Visible ozone injury on forest trees in Great Smoky Mountains National Park, USA. Water Air and Soil Pollution 116, 255-260.

Chappelka, A., Renfro, J., Somers, G. & Nash, B. (1997): Evaluation of ozone injury on foliage of black cherry (Prunus serotina) and tall milkweed (Asclepias exaltata) in Great Smoky Mountains National Park. Environmental Pollution 95, 13-18.

Chappelka, A., Skelly, J., Somers, G., Renfro, J. & Hildebrand, E. (1999b): Mature black cherry used as a bioindicator of ozone injury. Water Air and Soil Pollution 116, 261-266.

Chappelka, A. H., Somers, G. L. & Renfro, J. R. (2007): Temporal patterns of foliar ozone symptoms on tall milkweed (Asclepias exaltata L.) in Great Smoky Mountains National Park. Environmental Pollution 149, 358-365.

Chappelka, A. H., Neufeld, H. S., Davison, A. W., Somers, G. L. & Renfro, J. R. (2003): Ozone injury on cutleaf coneflower (Rudbeckia laciniata) and crown-beard (Verbesina occidentalis) in Great Smoky Mountains National Park. Environmental Pollution 125, 53-59.

Christensen, G. A., Campbell, S. J. & Fried, J. S. (2008): California's forest resources, 2001-2005: five-year Forest Inventory and Analysis report. U S Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR

Cobb, F. W. & Stark, R. W. (1970): Decline and mortality of smog-injured ponderosa pine. Journal of Forestry 68, 147-&.

Cobb, F. W., Wood, D. L., Stark, R. W. & Parmeter, J. R. (1968): Theory on relationships between oxidant injury and bark beetle infestation. Hilgardia 39, 141-152.

Dahlsten, D. L., Rowney, D. L. & Kickert, R. N. (1997): Effects of oxidant air pollutants on western pine beetle (Coleoptera: Scolytidae) populations in southern California. Environmental Pollution 96, 415-423.

Davis, D. D. (2007a): Ozone Injury to plants within the Seney National Wildlife Refuge in northern Michigan. Northeastern Naturalist 14, 415-424.

Davis, D. D. (2007b): Ozone-induced symptoms on vegetation within the Moosehorn National Wildlife Refuge in Maine. Northeastern Naturalist 14, 403-414.

Davis, D. D. (2009): Ozone-Induced Stipple on Plants in the Cape Romain National Wildlife Refuge, South Carolina. Southeastern Naturalist 8, 471-478.

Davis, D. D. (2011): Ozone-induced Leaf Symptoms on Vegetation in the Mingo National Wildlife Refuge, Missouri. Northeastern Naturalist 18, 115-122.

Davis, D. D. & Orendovici, T. (2006): Incidence of ozone symptoms on vegetation within a National Wildlife Refuge in New Jersey, USA. Environmental Pollution 143, 555-564.

Davison, A. W., Neufeld, H. S., Chappelka, A. H., Wolff, K. & Finkelstein, P. L. (2003): Interpreting spatial variation in ozone symptoms shown by cutleaf cone flower, Rudbeckia laciniata L. Environmental Pollution 125, 61-70.

Duchelle, S., Skelly, J. & Chevone, B. (1982): Oxidant effects on forest tree seedling growth in the Appalachian mountains. Water Air and Soil Pollution 18, 363-373.

Duchelle, S. F., Skelly, J. M., Sharick, T. L., Chevone, B. I., Yang, Y. S. & Nellessen, J. E. (1983): Effects of ozone on the productivity of natural vegetation in a high meadow of the Shenandoah-National-Park of Virginia. Journal of Environmental Management 17, 299-308.

Eatough Jones, M., Paine, T. D., Fenn, M. E. & Poth, M. A. (2004): Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. Forest Ecology and Management 200, 67-76.

Fenn, M. E. & Dunn, P. H. (1989): Litter decomposition across an air-pollution gradient in the San Bernardino Mountains. Soil Science Society of America Journal 53, 1560-1567.

Fenn, M. E. & Bytnerowicz, A. (1993): Dry deposition of nitrogen and sulfur to ponderosa and jeffrey pine in the San-Bernardino National Forest in Southern California. Environmental Pollution 81, 277-285.

Ferretti, M., Calderisi, M. & Bussotti, F. (2005): Were there significant changes in the overall condition of the CONECOFOR plots over the 1995-2005 period? Annali dell'Istituto Sperimentale per la Selvicoltura 34, 101-113.

Ferretti, M., Calderisi, M. & Bussotti, F. (2007a): Ozone exposure, defoliation of beech (Fagus sylvatica L.) and visible foliar symptoms on native plants in selected plots of South-Western Europe. Environmental Pollution 145, 644-651.

Ferretti, M., Bussotti, F., Fabbio, G. & Petriccione, B. (2003a): Ozone levels, actual and potential effects on the vegetation at the permanent monitoring plots of the CONECOFOR programme in Italy - Achievements, problems and perspectives. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 121-126.

Ferretti, M., Gerosa, G., Bussotti, F. & Fabbio, G. (2003b): Ozone exposure, crown transparency and basal area increment at the permanent monitoring plots of the CONECOFOR programme in Italy. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 107-119.

Ferretti, M., Bussotti, F., Fabbio, G. & Petriccione, B. (2006a): Biodiversity status and changes in the permanent monitoring plots of the CONECOFOR programme - Achievements, problems, perspectives. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 107-111.

Ferretti, M., Bussotti, F., Campetella, G., Canullo, R., Chiarucci, A., Fabbio, G. & Petriccione, B. (2006b): Biodiversity - its assessment and importance in the Italian programme for the intensive monitoring of forest ecosystems CONECOFOR. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 3-16.

Ferretti, M., Bussotti, F., Calatayud, V., Sanz, M. J., Schaub, M., Krauchi, N., Petriccione, B., Sanchez-Pena, G. & Ulrich, E. (2007b): Ozone and forests in South-Western Europe. Environmental Pollution 145, 617-619.

Ferretti, M., Bussotti, F., Calatayud, V., Schaub, M., Krauchi, N., Petriccione, B., Sanchez-Pena, G., Sanz, M. J. & Ulrich, E. (2007c): Ozone and forests in South-Western Europe - What have we learned? Environmental Pollution 145, 652-655.

FIMCI, F. I. M. C. I.,editors (2003): Intensive Monitoring of Forest Ecosystems in Europe, Technical Report 2003. EC-UN/ECE, Brussels, Geneva, 2003.

Gerosa, G. & Anfodillo, T. (2003): Modelling stomatal uptake of ozone: data requirements and applicability to the CONECOFOR PMPs in Italy. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 85-97.

Gerosa, G., Ferretti, M., Buffoni, A. & Spinazzi, F. (2003): Vegetation exposure to ozone at the permanent monitoring plots of the CONECOFOR Programme in Italy: estimating AOT40 by means of passive samplers. Annali dell'Istituto Sperimentale per la Selvicoltura 30, 53-62.

Gimeno, B. S., Penuelas, J., Porcuna, J. L. & Reinert, R. A. (1995): Biomonitoring ozone phytotoxicity in eastern Spain. Water Air and Soil Pollution 85, 1521-1526.

Girgzdiene, R., Serafinaviciute, B., Stakenas, V. & Bycenkiene, S. (2009): Ambient Ozone Concentration and Its Impact on Forest Vegetation in Lithuania. Ambio 38, 432-436.

Godzik, B. & Grodzinska, K. (2002): Ground level ozone concentration and its effect on plants of polish national parks. Kosmos 5, 427.

Godzik, S. & Sienkiewicz, J. (1990): Air pollution and forest health in Central Europe: Poland, Czechoslovakia and German Democratic Republic. In: Ecological Risks - Perspectives from Poland and the United States (ed. by W. Grodzinski, E. Cowling &A. I. Breymeyer), National Academy Press, Washington D.C., pp. 155-170.

Gravano, E., Bussotti, F., Strasser, R. J., Schaub, M., Novak, K., Skelly, J. & Tani, C. (2004): Ozone symptoms in leaves of woody plants in open-top chambers: ultrastructural and physiological characteristics. Physiologia Plantarum 121, 620-633.

Grodzinska, K., Godzik, B., Fraczek, W., Badea, O., Oszlanyi, J., Postelnicu, D. & Shparyk, Y. (2004): Vegetation of the selected forest stands and land use in the Carpathian Mountains. Environmental Pollution 130, 17-32.

Grodzinska, K., Godzik, B., Badea, O., Barancok, P., Istona, J., Matejka, K., Moravcik, P., Niemtur, S., Oszlanyi, J., Parpan, V., Varsavova, M., Bytnerowicz, A. & Szaro, R. (2002): Vegetation of selected forest stands in the Carpathian mountains. In: Effects of air pollution on forest health and biodiversity in forests of the Carpathian Mountains. Proceedings of the NATO Advanced Research Workshop, Stara Lesna, Slovakia, 22-26 May 2002 (ed. by R. C. Szaro, A. Bytnerowicz &J. Oszlanyi), pp. 96-117.

Grodzińska, K. & Szarek-Łukaszewska, G. (1997): Polish Mountain Forests: Past, Present and Future. Environmental Pollution 98, 369-374.

Grodzki, W. (2007): Spatio-temporal patterns of the Norway spruce decline in the Beskid Slaski and Zywiecki (Western Carpathians) in southern Poland. Journal of Forest Science (Prague) 53, 38-44.

Grodzki, W., McManus, M., Knizek, M., Novotny, J., Meshkova, V., Mihalciuc, V. & Slobodyan, Y. (2002): The Response of Ips typographus (L.) Populations in Polluted and Non-Polluted Spruce Stands in the Carpathian Mountain Region.

Grodzki, W., McManus, M., Knizek, M., Meshkova, V., Mihalciuc, V., Novotny, J., Turcani, M. & Slobodyan, Y. (2004): Occurrence of spruce bark beetles in forest stands at different levels of air pollution stress. Environmental Pollution 130, 73-83.

Grulke, N. E. (1999): Physiological responses of Ponderosa pine to gradients of environmental stressors. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. M. J. R. Miller), pp. 126-163.

Grulke, N. E., Andersen, C. P., Fenn, M. E. & Miller, P. R. (1998): Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. Environmental Pollution 103, 63-73.

Harris, T. B., Rajakaruna, N., Nelson, S. J. & Vaux, P. D. (2012): Stressors and threats to the flora of Acadia National Park, Maine: Current knowledge, information gaps, and future directions. Journal of the Torrey Botanical Society 139, 323-344.

Hildebrand, E., Skelly, J. M. & Fredericksen, T. S. (1996): Foliar response of ozone sensitive hardwood tree species from 1991 to 1993 in the Shenandoah National Park, Virginia. Canadian Journal of Forest Research 26, 658-669.

Huettl, R. F., Fink, S., Lutz, H. J., Poth, M. & Wisniewski, J. (1990): Forest decline, nutrient supply and diagnostic fertilization in southwestern Germany and in southern California. Forest Ecology and Management 30, 341-350.

Innes, J., Skelly, J. & Schaub, H. (2001): Ozone and broadleaved species - A guide to the identification of ozone-induced foliar injury. Haupt, Birmensdorf, Eidgenössische Foschungsanstalt WSL. Bern, Stuttgart, Wien.

Jacobson, J. S. & Hill, A. C. (1971): Recognition of air pollution injury to vegetation: a pictorial atlas.

Jones, M. E. & Paine, T. D. (2006): Detecting changes in insect herbivore communities along a pollution gradient. Environmental Pollution 143, 377-387.

Karlsson, P. E., Örlander, G., Langvall, O., Uddling, J., Hjorth, U., Wiklander, K., Areskoug, B. & Grennfelt, P. (2006): Negative impact of ozone on the stem basal area increment of mature Norway spruce in south Sweden. Forest Ecology and Management 232, 146-151.

Kickert, R. N. & Krupa, S. V. (1990): Forest responses to tropospheric ozone and global climate change - an analysis. Environmental Pollution 68, 29-65.

Klap, J. M., Oude Voshaar, J. H., De Vries, W. & Erisman, J. W. (2000): Effects of Environmental Stress on Forest Crown Condition in Europe. Part IV: Statistical Analysis of Relationships. Water, Air, and Soil Pollution 119, 387-420.

Kline, L. J., Davis, D. D., Skelly, J. M., Savage, J. E. & Ferdinand, J. (2008): Ozone sensitivity of 28 plant selections exposed to ozone under controlled conditions. Northeastern Naturalist 15, 57-66.

Kohut, R. (2007): Assessing the risk of foliar injury from ozone on vegetation in parks in the U.S. National Park Service's Vital Signs Network. Environmental Pollution 149, 348-357.

Kohut, R., Flanagan, C., Cheatham, J. & Porter, E. (2012): Foliar ozone injury on cutleaf coneflower at Rocky Mountain National Park, Colorado. Western North American Naturalist 72, 32-42.

Krause, G. H. M., Jung, K. D. & Prinz, B. (1985): Experimental studies on the causes of forest dieback in West Germany

Experimentelle Untersuchungen zur Aufklarung der neuartigen Waldschaden in der Bundesrepublik Deutschland. In Forest dieback: influencing factors and their evaluation. Proceedings of a symposium held at Goslar, W. Germany, 18-20 June 1985. VDI-Berichte, 627-656.

Krause, G. H. M., Arndt, U., Brandt, C. J., Bucher, J., Kenk, G. & Matzner, E. (1986): Forest decline in Europe - development and possible causes. Water Air and Soil Pollution 31, 647-668.

Lee, E. H., Tingey, D. T., Hogsett, W. E. & Laurence, J. A. (2003): History of tropospheric ozone for the San Bernardino Mountains of Southern California, 1963-1999. Atmospheric Environment 37, 2705-2717.

Lefohn, A. S., Jackson, W., Shadwick, D. S. & Knudsen, H. P. (1997): Effect of surface ozone exposures on vegetation grown in the Southern Appalachian Mountains: Identification of possible areas of concern. Atmospheric Environment 31, 1695-1708.

Linzon, S. N. (1966): Damage to eastern white pine by sulfur dioxide, semimature-tissue needle blight, and ozone. Journal of the Air Pollution Control Association 16, 140-144.

Lorenz, M. (1995): International co-operative programme on assessment and monitoring of air pollution effects on forests - ICP forests. Water Air and Soil Pollution 85, 1221-1226.

Lorenz, M. & Mues, V. (2007): Forest health status in Europe. Thescientificworldjournal 7, 22-27.

Lorenz, M., Becher, G., Mues, V., Fischer, R., Becker, R., Catalayud, V., Dise, N., Krause, G. H. M., Sanz, M. & Ulrich, E. (2005): Forest Condition in Europe, Technical Report of IOCP Forests. Federal Research Centre for Forestry and Forest Products (BFH) and Department of Wood Science University of Hamburg, Hamburg.

Luck, R. F. (1976): Bionomics and parasites of a needle miner, Coleotechnites sp, Gelechiidae lepidoptera infesting Jeffrey pine in Southern-California. Environmental Entomology 5, 937-942.

Luck, R. F. (1980): Impact of Oxidant Air Pollution on Ponderosa and Jeffrey Pine Cone Production. Effects of air pollutants on Mediterranean and temperate forest ecosystems (ed. by P. Miller), pp. 240. Riverside, California, U.S.A.

Mangoni, M. & Buffoni, A. (2005): Status and trend of ground-level ozone at the CONECOFOR plots, 1996-2005. Annali dell'Istituto Sperimentale per la Selvicoltura 34, 85-99.

Manning, W. J., Godzik, B. & Musselman, R. (2002): Potential bioindicator plant species for ambient ozone in forested mountain areas of central Europe. Environmental Pollution 119, 283-290.

Matyssek, R. & Innes, J. L. (1999): Ozone - A risk factor for trees and forests in Europe? Water Air and Soil Pollution 116, 199-226.

McBride, J. R. & Miller, P. R. (1987): Responses of American forests to photochemical oxidants. Springer-Verlag.

McBride, J. R. & Laven, R. D. (1999): Impact of oxidant air pollutants on forest succession in the mixed conifer forests of the San Bernardino mountains.

McBride, J. R., Semion, V. P. & Miller, P. R. (1975): Impact of air-pollution on the growth of ponderosa pine. California Agriculture 29, 8-9.

McLaughlin, S. B., Nosal, M., Wullschleger, S. D. & Sun, G. (2007): Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. New Phytologist 174, 109-124.

Miller, D. E. & Watmough, S. A. (2009): Air pollution, climate, soil acidity, and indicators of forest health in Ontario's sugar maple forests. Canadian Journal of Forest Research 39, 2065-2079.

Miller, P., Guthrey, R., Schilling, S. & Carroll, J. (1998a): Ozone injury responses of ponderosa and Jeffrey pine in the Sierra Nevada and San Bernardino Mountains in California. General Technical Report - Pacific Southwest Research Station, USDA Forest Service, 35-42.

Miller, P., Bytnerowicz, A., Fenn, M., Poth, M., Temple, P., Schilling, S., Jones, D., Johnson, D., Chow, J. & Watson, J. (1998b): Multidisciplinary study of ozone, acidic deposition and climate effects on a mixed conifer forest in California, USA. Chemosphere 36, 1001-1006.

Miller, P. R. (1973): Oxidant-induced community change in a mixed conifer forest. In: Air Pollution Damage to Vegetation, Advances in Chemistry Series 122, pp. 101-117.

Miller, P. R. (1985): Ozone effects in the San Bernardino National Forest. In: Air pollution and the productivity of the forest. Symposium held Washington, DC, Oct. 4 and 5, 1983 (ed. by D. D. Davis, A. A. Millen &L. Dochinger), pp. 161-197.

Miller, P. R. & McBride, J. R. (1975): Effects of air pollutants on forests. In: Responses of plants to air pollutants (ed. by J. B. Mudd &T. T. Kozlowski), Academic Press, New York, pp. 195-235.

Miller, P. R. & Rechel, J. (1999): Temporal Changes in Crown Condition Indices, Needle Litterfall, and Collateral Injuries of Ponderosa and Jeffrey Pines. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. Miller &J. R. Mcbride), Springer, New York, NY, pp. 164-178.

Miller, P. R. & Arbaugh, M. J. (2000): Ozone impacts on California forests.

Miller, P. R., Arbaugh, M. J. & Temple, P. J. (1997): Ozone and its known and potential effects on forests in western United States. In: Ecological Studies Volume 127: Forest decline and ozone. A comparison of controlled chamber and field experiments., pp. 39-67.

Miller, P. R., Taylor, O. C., Parmeter, J. R. & Cardiff, E. A. (1963): Ozone injury to foliage of Pinus ponderosa. Phytopathology 53, 1072-&.

Miller, P. R., Stolte, K. W., Duriscoe, D. M. & Pronos, J. (1996): Evaluating ozone air pollution effects on pines in the western United States. General Technical Report - Pacific Southwest Research Station, USDA Forest Service, iv + 79 pp.-iv + 79 pp.

Miller, P. R., Kickert, R. N., Taylor, O. C., Arkley, R. J., Cobb, F. W. J., Dahlsten, D. L., Gersper, P. J., Luck, R. F., McBride, J. R., Parmeter, J. R., Wenz, J. M., White, M. & Wilcox, W. W. (1977): Photochemical oxidant air pollution effects on a mixed conifer forest ecosystem - a progress report. University of California, Riverside and Berkeley.

Minnich, R. A. (1999): Vegetation, Fire Regimes, and Forest Dynamics. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. Miller &J. R. Mcbride), Springer, New York, NY pp. 44-78.

Moravcik, P., Bytnerowicz, A., Cerny, M. & Musselmann, R. (2002): Ozone distribution and effects in the Sumava mountains, Czech Republic.

Muzika, R. M., Guyette, R., Zielonka, T. & Liebhold, A. (2002): The influence of air pollution on tree growth in the Carpathian mountains. In: Effects of air pollution on forest health and biodiversity in forests of the Carpathian Mountains. Proceedings of the NATO Advanced Research Workshop, Stara Lesna, Slovakia, 22-26 May 2002 (ed. by R. C. Szaro, A. Bytnerowicz &J. Oszlanyi), pp. 185-193.

Muzika, R. M., Guyette, R. P., Zielonka, T. & Liebhold, A. M. (2004): The influence of O(3), NO(2) and SO(2) on growth of Picea abies and Fagus sylvatica in the Carpathian Mountains. Environmental Pollution 130, 65-71.

Nash, T. H., III & Sigal, L. L. (1999): Epiphytic lichens in the San Bernardino Mountains in relation to oxidant gradients. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. M. J. R. Miller), pp. 223-234.

National Research Council, editors (1977): Ozone and other photochemical oxidants.National Academy Press, Washington D.C.

Naveh, Z., Steinberger, E. H., Chaim, S. & Rotmann, A. (1980): Photochemical air-pollutants - a threat to Mediterranean coniferous forests and upland ecosystems. Environmental Conservation 7, 301-309.

Neufeld, H. S., Renfro, J. R., Haecker, W. D. & Silsbee, D. (1992): Ozone in the Great Smoky Mountains National Park: dynamics and effects on plants. In: Tropospheric Ozone ans the Environment II (ed. by R. D. Berglund), Aie and Waste Management Association Press, Pittsburgh, P.A., pp. 594-617.

Neufeld, H. S., Peoples, S. J., Davison, A. W., Chappelka, A. H., Somers, G. L., Thomley, J. E. & Booker, F. L. (2012): Ambient ozone effects on gas exchange and total non-structural carbohydrate levels in cutleaf coneflower (Rudbeckia laciniata L.) growing in Great Smoky Mountains National Park. Environmental Pollution 160, 74-81.

Oszlányi, J. (1997): Forest Health and Environmental Pollution in Slovakia. Environmental Pollution 98, 389-392.

Ozolincius, R. & Serafinaviciute, B. (2003): Ozone-induced visible foliar injuries in Lithuania. Baltic Forestry 9, 51-57.

Ozolincius, R., Stakenas, V. & Serafinaviciute, B. (2005): Meteorological factors and air pollution in Lithuanian forests: Possible effects on tree condition. Environmental Pollution 137, 587-595.

Paoletti, E. (2007): Ozone impacts on forests. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2, 13 pp.

Peterson, D. L. & Arbaugh, M. J. (1988): An evaluation of the effects of ozone injury on radial growth of ponderosa pine (Pinus ponderosa) in the southern Sierra-Nevada. Japca-the International Journal of Air Pollution Control and Hazardous Waste Management 38, 921-927.

Peterson, D. L., Arbaugh, M. J. & Robinson, L. J. (1991): Regional growth changes in ozone-stressed ponderosa pine (Pinus ponderosa) in the Sierra Nevada, California, USA. The Holocene 1, 50-61.

Peterson, D. L., Arbaugh, M. J., Wakefield, V. A. & Miller, P. R. (1987): Evidence of growth reduction in ozone-injured jeffrey pine (Pinus jeffreyi Grev. and Balf.) in Sequoia and Kings Canyon National-Parks. Japca-the International Journal of Air Pollution Control and Hazardous Waste Management 37, 906-912.

Peterson, D. L., Silsbee, D. G., Poth, M., Arbaugh, M. J. & Biles, F. E. (1995): Growth-response of bigcone douglas-fir (Pseudotsuga macrocarpa) to long-term ozone exposure in southern California. Journal of the Air & Waste Management Association 45, 36-45.

Prinz, B. (1985): Effects of air-pollution on forests - critical-review. Journal of the Air Pollution Control Association 35, 913-915.

Prinz, B. (1988): Ozone effects of vegetation. In: Tropospheric Ozone Regional and Global Scale Interactions (ed. by I. S. A. Isaksen), pp. 161-184.

Pronos, J., Merrill, L. & Dahlsten, D. (1999): Insects and pathogens in a pollution-stressed forest. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. M. J. R. Miller), pp. 317-337.

Purdon, M., Cienciala, E., Metelka, V., Beranová, J., Hunová, I. & Cerny, M. (2004): Regional variation in forest health under long-term air pollution mitigated by lithological conditions. Forest Ecology and Management 195, 355-371.

Rehfuess, K. E. (1987): Perceptions on Forest Diseases in Central Europe. Forestry 60, 1.

Richards, B. L., Taylor, O. C. & Edmunds, G. F. (1968): Ozone needle mottle of pine in southern California. Journal of the Air Pollution Control Association 18, 73-77.

Sanchez Gimeno, B., Velissariou, D., Barnes, J. D., Inclan, R., Pena, J. M. & Davison, A. (1992): Visible ozone damage in needles of Pinus halepensis in Greece and Spain. Ecologia 6, 131-134.

Sanz, M. J., Calatayud, V. & Calvo, E. (1999): Spatial pattern of ozone injury in Aleppo pine and air pollution dynamics in the Mediterranean. Physics and Chemistry of the Earth Part C-Solar-Terrestial and Planetary Science 24, 495-498.

Sanz, M. J., Calatayud, V. & Calvo, E. (2000): Spatial pattern of ozone injury in Aleppo pine related to air pollution dynamics in a coastal-mountain region of eastern Spain. Environmental Pollution 108, 239-247.

Schmieden, U. & Wild, A. (1995): The contribution of ozone to forest decline. Physiologia Plantarum 94, 371-378.

Sigal, L. L. & Nash, T. H. (1983): Lichen communities on conifers in Southern-California Mountains - an ecological survey relative to oxidant air-pollution. Ecology 64, 1343-1354.

Silaghi, D. & Badea, O. (2012): Monitoring of ozone in selected forest ecosystems in Southern Carpathian and Romanian Intensive Monitoring Network (level II). Journal of Environmental Monitoring 15, 1710-1717.

Skelly, J. M. & Johnston, J. W. (1977): A status report of the deterioration of eastern white pine due to oxidant air pollution in the Blue Ridge Mountains of Virginia. Proceedings of the American Phytopathological Society 4, 86-87.

Skelly, J. M., Innes, J. L., Savage, J. E., Snyder, K. R., Vanderheyden, D., Zhang, J. & Sanz, M. J. (1999): Observation and confirmation of foliar ozone symptoms of native plant species of Switzerland and southern Spain. Water Air and Soil Pollution 116, 227-234.

Smith, G., Coulston, J., Jepsen, E. & Prichard, T. (2003): A national ozone biomonitoring program - Results from field surveys of ozone sensitive plants in northeastern forests (1994-2000). Environmental Monitoring and Assessment 87, 271-291.

Somers, G. L., Chappelka, A. H., Rosseau, P. & Renfro, J. R. (1998): Empirical evidence of growth decline related to visible ozone injury. Forest Ecology and Management 104, 129-137.

Souza, L., Neufeld, H. S., Chappelka, A. H., Burkey, K. O. & Davison, A. W. (2006): Seasonal development of ozone-induced foliar injury on tall milkweed (Asclepias exaltata) in Great Smoky Mountains National Park. Environmental Pollution 141, 175-183.

Stark, R. W. & Cobb, F. W. (1969): Smog injury, root diseases and bark beetle damage in ponderosa pine. California Agriculture 23, 13-15.

Stark, R. W., Miller, P. R., Cobb, F. W., Wood, D. L. & Parmeter, J. R. (1968): Incidence of bark beetle infestation in injured trees. Hilgardia 39, 121-.

Swank, W. T. & Vose, J. M. (1990): Watershed-scale responses to ozone events in a Pinus strobus L. plantation. Water Air and Soil Pollution 54, 119-133.

Szaro, R., Bytnerowicz, A. & Oszlanyi, J. (2002): Effects of air pollution on forest health and biodiversity in forests of the Carpathian mountains: an overview. *In* Effects of air pollution on forest health and biodiversity in forests of the Carpathian Mountains. Proceedings of the NATO Advanced Research Workshop, Stara Lesna, Slovakia, 22-26 May 2002 (ed. by R. C. Szaro, A. Bytnerowicz &J. Oszlanyi), pp. 3-12.

Takemoto, B. K., Bytnerowicz, A. & Fenn, M. E. (2001): Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests. Forest Ecology and Management 144, 159-173.

Taylor, O. C. (1973): Oxidant air pollution effects on a western coniferous forest ecosystem. Air Pollution Research Center, University of California, Riverside.

Temple, J. P. (1999): Effects of ozone on understory vegetation in the mixed conifer forest. In: Ecological Studies Vol. 134: Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains (ed. by P. R. Miller &J. R. Mcbride), Springer, New York, NY

Temple, P., Bytnerowicz, A., Fenn, M. & Poth, M. (2005): Air Pollution Impacts in the Mixed Conifer Forests of Southern California. USDA Forest Service General Technical Report, 145-164.

Ulrich, B. (1990): Waldsterben - forest decline in West-Germany. Environmental Science & Technology 24, 436-441.

Velissariou, D., Davison, A. W., Barnes, J. D., Pfirrmann, T., Maclean, D. C. & Holevas, C. D. (1992): Effects of air-pollution on Pinus halepensis (Mill.) - pollution levels in Attica, Greece. Atmospheric Environment Part a-General Topics 26, 373-380.

Vollenweider, P., Ottiger, M. & Gunthardt-Goerg, M. S. (2003): Validation of leaf ozone symptoms in natural vegetation using microscopical methods. Environmental Pollution 124, 101-118.

Weinstein, D. A., Laurence, J. A., Retzlaff, W. A., Kern, J. S., Lee, E. H., Hogsett, W. E. & Weber, J. (2005): Predicting the effects of tropospheric ozone on regional productivity of ponderosa pine and white fir. Forest Ecology and Management 205, 73-89.

Wienhaus, O. (2003): Forest damage situation and its development in East Germany. AFZ/Der Wald, Allgemeine Forst Zeitschrift fur Waldwirtschaft und Umweltvorsorge 58, 1314-1315.

Wieser, G., Manning, W. J., Tausz, M. & Bytnerowicz, A. (2006): Evidence for potential impacts of ozone on Pinus cembra L. at mountain sites in Europe: An overview. Environmental Pollution 139, 53-58.

Williams, W. & MacGregor, N. (1975): Oxidant induced air pollution damage to forest trees in the southern Sierra-Nevada Mountains of California. Proceedings of the American Phytopathological Society 2, 120.

Williams, W. T., Brady, M. & Willison, S. C. (1977): Air-pollution damage to forests of Sierra-Nevada Mountains of California. Journal of the Air Pollution Control Association 27, 230-234.

8 Summary and final conclusion

Biodiversity is the variety of life on Earth and includes three levels: the diversity of ecosystems, species diversity, and genetic diversity within species. Furthermore, it comprises functional interactions amongst organisms as being integrated in their respective ecological compartment. The aim of this study was to assess the consequences of ozone-induced impacts on the genetic, structural and functional grounds of biodiversity. This analysis was done through a literature research covering the period of 1980 -2014, by more than 1000 publications.

Among the available dataset of literature the term biodiversity was used in different ways with only a small number of studies being designed specifically with the aim of clarifying ozone impacts on biodiversity. The use of complex experimental setups, the limited availability of suitable experimental plots and the need to consider prolonged periods of observation appear as causes of the lack of reliable data bases. Thus, the literature research compiled the available knowledge on differential ozone sensitivity at the species-level up to the effects of ozone at the ecosystem-level, highlighting ecosystem functions and services that have been investigated and evaluated.

The current knowledge is based on extensive data bases about the ozone sensitivity of plant receptors. Worldwide information is available about 343 varieties across 53 crop plant species and about 464 vascular and fern plant species belonging to the (semi)-natural vegetation (298 herbaceous and 164 woody plant species) out of these, 265 are native to Germany. Nevertheless, the ozone studies have only covered a small fraction of the entire flora to date i.e. approximately 6.5 % of the plant species in Germany.

About two third of woody and about one half of herbaceous species have been described as ozone sensitive in one study at least. The proportion is slightly higher for visible leaf injury than for growth effects, herbs and deciduous woods are more responsive than grasses and coniferous tress, respectively. Several plant families have been identified which showed an increased proportion of sensitive species or genotypes, however, no significant relationship between ecological traits and the ozone-sensitivity could be found.

Intra-specific variations of ozone sensitivity of vascular plants have been frequently studied in terms of either temporal or spatial differentiation. There is some evidence that ozone pollution in the past already has affected plant selection and modified the genetic pool of ozone sensitive genotypes.

Information on species other than vascular plants is rather poor; especially, there is a lack of experimental studies on other species in terms of their ecological risk within the ecosystem due to ozone.

Case studies conducted along ozone gradients to assess ecosystem effects of ozone were mostly conducted at locations in North America and Europe. In establishing cause-effect relationships associated with ozone stress numerous assessment approaches have been employed. Ozone-specific visible macroscopic leaf injury was identified in 258 herbaceous species, although such findings have little importance for ecosystem functionality.

More substantial parameters such as the habitat structure and species composition of communities and the abundance of different species or functional groups were differently assessed for plants, insects, soil organisms and microorganisms, mainly as part of fumigation experiments. In many cases the influence of ozone stress on different ecosystem compartments could be shown.

For both, grassland and forest ecosystems there is increasing evidence that ozone may affect the competitive balance of a two-species model system. The predominant response of grassland communities to long-term fumigation was a decline in the most sensitive species associated with an increase in the more tolerant one, thus the resulting answer of the total community was determined by the sensitivity of its components. In general, old and species rich grassland communities of low productivity exhibited a low susceptibility to ozone.

Experiments on forest communities clearly showed that high levels of ozone have the potential to alter the strength of intraspecific competition within aspen populations and the interspecific competition between tree species (aspen / birch or beech / spruce). Moreover, understory vegetation may be influenced when overstory trees had been impacted by ozone. The findings demonstrate the complexity in response patterns of a plant community with respect to its species composition.

At least for crops and trees, experimental studies clearly indicate that ozone may affect the plant-pathogen interaction by either predispose or harden plants to pathogen attack. Hence, there exists no consistent prediction whether a given ozone scenario will lead to an increased or decreased disease incidence, at present. As both stressors are known to induce the same defence mechanisms atmospheric ozone may alter the co-evolutionary relationship of plant-pathogen interactions in the future.

The impact of elevated ozone on plant-parasite interactions is highly variable. However, there is evidence that the biodiversity of forest insect communities is likely to change under atmospheric conditions predicted for the future with further consequences for nutrient cycling in ecosystems.

Documented effects of elevated ozone on composition of communities of soil organisms (invertebrates and microorganisms) were consistently shown to be the result of changes in the interactions with ozone-affected plants and seem to be attributed to plant-mediated shifts in substrate balance.

The harmful effect of ozone to impair stomatal control and to cause a sluggish stomatal response has been shown for a number of tree and herbaceous plant species. As a consequence, ozone may upset the water balance of the whole plant and predispose vegetation to drought stress in forests and grasslands. At the landscape-level, this change in plant water use together with a changed streamflow was assumed to lead to further impacts on the hydrological cycle. Using stand-level simulation models plant's water use was estimated to be either increased or reduced by up to 7 %.

Recent findings indicate that rising levels of ozone may have potential impacts on terrestrial carbon sinks by reducing the capability of vegetation to assimilate carbon. In consequence, soil carbon formation rates were lowered and more CO_2 accumulates in the atmosphere. Therefore, it is suggested that global-scale reductions of productivity of terrestrial ecosystems (mainly forests) indirectly contribute to climate change and global warming.

It further has been shown that elevated levels of ozone interfere with phytogenic VOCs in different ways. In general, ozone-induced changes in timing of flowering and signalling could have large ecological impacts, affecting plant pollination, the food supply of nectar feeding insects or defence against herbivory insects.

Thus, ozone exposure can induce production loss, change resource allocation within plants and affect ecosystem hydrology, as well as the reproductive capacity of individual plants, which has important implications for structure and functions of the entire species community.

In conclusion, the potentially adverse effects of ozone on vegetation are comprehensively documented in the present study. While the interest related to ozone effects on crops and commercially relevant trees has mainly been driven by concerns about the potential economic losses, the more recent emphasis in assessing potential ozone effects on ecosystem integrity and related ecosystem functions and services is based on concerns of the potential threats of ozone to the biodiversity of these habitats, and the long-term, more subtle impacts on ecosystem functions and services such as carbon sequestration, nutrient cycling, water relations and pollination. Directly related to ecosystem structure and functioning an assessment of impacts of ozone on the genetic diversity in forestry and semi-natural ecosystems is necessary. This study referred on research results that clearly documented a potential impact of current and future ozone levels on processes, biotic interactions, structure and functioning of terrestrial ecosystems with vascular plants playing a central role as sensitive receptors. It also brought out, that there is an urgent need of applying more holistic approaches to investigate the plant's response within its complex and natural ecosystem and environment.

There is clear evidence of a broad intraspecific variation of ozone sensitivity for plant species and we have to keep in mind that classifying a species as being either ozone sensitive or tolerant might be an oversimplification because the response of a genotype rather seems to reflect its own exposure history than a generic species specific trait and therefore represents one point within the amplitude describing a complex set of responses. In context with risk assessment approaches, furthermore, this range of responsiveness must be taken into account. Nevertheless, there is a number of plant species, which are endangered or near-threatened in Germany and simultaneously seemed to be ozone sensitive. Their habitats should be observed carefully in future in terms of ozone monitoring.

However, for most organisms populating our terrestrial ecosystems no information about their responsibility to ozone exists at all. For future research activities, more emphasis should be put on the soil food web and related processes and organisms to understand biotic interaction and flow of energy and nutrient and its sensitivity to ozone.

Moreover, in natural ecosystems individuals have to cope with abiotic stressors (e.g. drought, nutrient limitation, or elevated CO_2) which all might have the potential to modify individual's response to ozone. Exposure to ozone is known to interact with these modifying factors or conversely, the response of an individual or a population to ozone largely depend on the co-occurrence or absence of these stressors. Along with the increasing concern about climate change effects interaction with elevated atmospheric CO_2 concentrations is of particular importance. Consistent across different vegetation types and derived from various experimental approaches, there is evidence that elevated CO_2 has the potential to mitigate negative effects of ozone. Although the overall impact of climate change on future ozone effects is difficult to predict it is assumed that ozone risk assessments will considerably be influenced by changes in other climate change factors. However, a detailed review of these complex interactions went beyond the scope of this study.

With the exception of modelling water and carbon pools the description and evaluation of the various effects of ozone presented here are made in a qualitative way exclusively. Quantitative estimations and any kind of dose-response functions are still lacking for other endpoints than growth and transpiration and receptors other than crops, forest trees or some pasture plants. To estimate the risk to ecosystems and to establish critical levels for ozone to protect the integrity of natural ecosystems key species and key parameters within a model system have to be selected which are able to indicate a dysfunction of an ecosystem.