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Impact of tropospheric ozone on terrestrial biodiversity: A literature analysis to identify ozone sensitive taxa

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Summary

Tropospheric ozone has long been known as highly phytotoxic. However, currently hardly anything is known whether this air pollutant can also pose a threat to the overall biodiversity in terrestrial ecosystems. Identifying the relative ozone sensitivities of relevant taxa or species can be a first step in an assessment if biodiversity is at risk from ozone. A literature survey was conducted describing experimental and observational results of exposure of organisms and particularly plant species to ozone at environmentally relevant concentrations. For plants ozone effects considered were vegetative growth (e.g. biomass of shoots, foliage, single leaves, stems, and roots), reproduction (number and biomass of seeds and flowers), species development, and symptoms of visible foliar injury. A total of 474 literature references were evaluated which described such effects. For crop plants 54 species with 350 varieties could be considered, while (semi)natural vegetation was represented by 465 vascular plant species comprising 298 herbaceous and 165 woody plant species. Overall, these ozone studies cover only a small fraction of the entire global flora. About two third of woody and about one half of native herbaceous plant species investigated so far have been described as ozone sensitive in at least one study. Ozone sensitivity is slightly higher with respect to visible leaf injury as compared to growth effects, and herbs and deciduous tree species are more responsive than grasses and coniferous trees. Observational results from field surveys conducted along ozone gradients to assess ecosystem effects of ozone in North America and Europe revealed visible macroscopic leaf injuries for 258 herbaceous species. However, these findings often have not been verified under experimental ozone exposure. Albeit the numbers of ozone studies related to a particular plant family varied considerably, high proportions of ozone sensitive species were found e.g. for the families Myrtaceae, Salicaceae and Onograceae, while low proportions of ozone sensitive species were found e.g. for the families Brassicaceae, Boraginaceae and Plantaginaceae. Intra-specific variations of ozone sensitivity of vascular plants were primarily detected in crop species (e.g. wheat, soybean, snap bean, clover, rice), most often derived from screening studies of cultivars for their relative ozone sensitivity / tolerance to ozone. In some cases intra-specific variation of ozone sensitivity is also true for different populations of woody and herbaceous plant species, which often resulted from temporal or spatial differentiation of the relative ozone susceptibility. Therefore, there is some evidence that ozone pollution in the past has already affected plant selection and modified the genetic pool of ozone sensitive genotypes. Information on direct ozone effects on species other than vascular plants (e.g. ferns, mosses, fungi, algae, vertebrates) is very poor or irrelevant, i.e. ozone sensitivities for these taxa could not be described. This is also true for organisms like microbes, arthropods or insects which have not been tested so far for their responses to direct ambient ozone exposure. However, these organisms may be indirectly impaired by ozone via loss of vitality of the plant system to which they are associated.

1. Introduction

The loss of biological diversity (biodiversity) is one of the most prominent examples of global change. According to the definition of the Convention of Biological Diversity (CBD) biodiversity is defined as “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”. Significant drivers of the past and current loss of biodiversity are land use changes, changes of climate and atmospheric chemistry, invasive species, as well as soil and air pollution (SALA et al., 2000). While there is already scientific evidence and public awareness, respectively, that climate change or excessive deposition of nitrogen from the atmosphere must be regarded as major threats to biodiversity (CBD; STEVENS et al., 2010A; STEVENS et al., 2010B), there is currently little information if and to what extent biodiversity is at risk from tropospheric or ground level ozone pollution. This lack of information is all the more serious as during the last 60 years there has been undeniable evidence that tropospheric ozone has significant adverse effects on plant growth, crop yields and forest health and that this air pollutant has emerged as a problem of global dimension (ROYAL SOCIETY, 2008).

Typical effects of ozone on sensitive species include alterations of carbon allocation patterns, symptoms of visible injury, enhanced senescence, reduced growth and yield, or reduced flowering and seed production. Each of these effects can impact on the vitality of component species in plant communities, which may have implications for biodiversity. Therefore, identifying and understanding the relative sensitivity of individual species and genotypes to ozone is a central prerequisite for estimating effects at the community and ecosystem level and for the development of critical ozone levels to protect vegetation. However, there are hardly any systematic assessments which taxa are particularly affected by ozone.

In the present study we summarize the existing information of the relative susceptibility of different vascular plant species and genotypes, respectively (native herbaceous plants, woody plant, agricultural plants) to near-ambient ozone concentrations and – based on this information – identify ozone sensitive taxa. We restrict our analysis to assessments of ozone effects on ecologically relevant parameters, i.e. biomass growth, productivity, reproduction, and easily accessible visible symptoms of the respective organisms and do not consider studies with a focus on physiological and biochemical ozone effects. While ozone effects on vascular plants provide the overwhelming majority of information of the ozone susceptibility of organisms in terrestrial ecosystems, we also reviewed existing information of ozone effects on non-vascular plant species and on other non-plant organisms.

In the following text we first provide short summaries of ozone pollution trends, methods to study its effects and its mechanism of effects on plant organisms. We then provide detailed information on the relative ozone susceptibilities of the different taxa for which ozone effects have been described.

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2 Ozone pollution trends

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/NO₂), volatile organic compounds (VOC), methane (CH₄) and carbon monoxide (CO) (STAEHELIN, 2003). These precursors are of natural or anthropogenic origin such as vehicles, power plants, biomass burning and all other forms of combustion. Naturally occurring global ground-level background ozone concentrations in the pre-industrial era ranged between approx. 5 - 20 parts per billion (ppb) (MARENCO et al., 1994). Since that time annual mean background ozone concentrations have increased to values between approx. > 20 - 45 ppb depending on the geographical location (VINGARZAN, 2004) with a rate of increase of 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. Very high concentrations episodically occur, but for large parts of Western Europe there has been a noticeable lack of the short-term high ozone concentrations that had previously been experienced. Future ozone levels will be determined by the trends of the emissions of the precursors and of temperature and solar radiation. 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 (JACOB and WINNER, 2009; PRATHER et al., 2003; VINGARZAN, 2004). On the other hand, a recently published model study predicted more moderate increases of ozone levels until 2050 (WILD et al., 2012). In Germany there was also a slight increase in the annual mean ozone concentration between 1990 and 2011, but in recent years it is not possible to identify such statistically significant trend (UBA, 2016). According to ANDERSSON and ENGARDT (2010) and PERCY et al. (2003) about 50% of forests worldwide are expected to be exposed to ozone concentrations above 60 ppb by 2100. Ground-level ozone concentrations influenced by human activities vary significantly with time (diurnally, seasonally, inter-annually) and with geographic location. 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, its 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 formation of high ozone concentrations depends on the local meteorology, the topography and the regional sources of ozone precursors. In Europe, the highest average ozone levels occur in Central and Southern Europe (ROYAL SOCIETY, 2008).

3 Methods to study ozone effects on plants and terrestrial eco-systems

Experimental techniques to expose single plants, plant communities and segments of ecosystems to ozone range from controlled-environment growth chambers, greenhouses, field chambers to open-air ozone exposure systems (WEIGEL et al., 2015). In these systems targeted ozone concentrations are supplied to the test organisms by adding ozone to either ambient or charcoal-filtered air. Most of the information of ozone effects on plants is derived from the use of various types of indoor and outdoor chambers. For example, laboratory fumigation chambers of various designs which provide highly reproducible environmental and ozone exposure conditions have widely

been used for assessing visible injury or physiological and biochemical ozone effects (HECK et al., 1978). However, due to different microclimatic conditions in these chambers compared to ambient air ("chamber effect") plants often show morphological or physiological differences compared to field-grown plants which modify the response to ozone.

Open-top field chambers (OTC, HEAGLE et al., 1973) 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). Open-top chambers offer the opportunity to expose individual plants, model ecosystems and canopies of field plots for one to several growing seasons to either ambient and filtered air or to elevated levels of ozone induced by ozone addition. 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 and HALE, 1997). Hemispherical greenhouses ("solar domes") represent another type of closed outdoor fumigation chambers that are used in the UK (LUCAS et al., 1987).

The necessity to avoid chamber effects and space limitations and to investigate ecosystems under in situ conditions in an undisturbed environment led to the development and utilisation of free-air ozone exposure systems (PERCY et al., 2010) which have been used in a very limited number of experiments. One type of a 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. This type of exposure systems has been used for ozone effects studies with soybean (MORGAN et al., 2004) and with young tree species (KARNOSKY et al., 1999; WATANABE et al., 2013). 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 and FABIAN (2002) and tested and used by MATYSSEK et al. (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 as well as biotic interactions (pollination, herbivory) can be investigated.

A second chamberless method to assess effects of ambient ozone levels on plants is the use of protecting chemicals against ozone stress (MANNING et al., 2011). While this approach has long been known but rarely been applied, it has recently been utilised again with crop species in Europe (MILLS and HARMENS, 2011) and Asia (OKSANEN et al., 2013; RAI and AGRAWAL, 2012) or with tree species (PAOLETTI, 2007; PAOLETTI et al. 2011).

Methods of ozone exposure where there is no manipulation of the ozone concentration surrounding the plants are field observations and ambient ozone gradient studies where impacts of current or past ozone exposure scenarios in complex ecosystems are monitored and assessed. For example, the survey of ozone-specific leaf injury symptoms is a common worldwide established tool to assess significant ozone-response relationships. Prominent examples, where forest tree species and ecosystem responses to ozone have been assessed using ozone gradient approaches are studies in the USA (MCLAUGHLIN et al., 2007; MILLER and MCBRIDE, 1999), in the Carpathian Mountains (BYTNEROWICZ et al., 2003) and in Italy (FERRETTI et al., 2005).

4 Mechanisms of ozone uptake and effects on biota

Terrestrial ecosystems are the major sink for tropospheric ozone and consequently, vegetation is at particular risk from this pollutant. With respect to vegetation the mechanisms of ozone uptake and its effects have predominantly been investigated for vascular plants and

will be briefly described here.

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. 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 (CAPE et al., 2009; CIESLIK, 2004).

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 and LENDZIAN, 1989; MASSMAN and GRANTZ, 1995). This transfer of the gas through the atmosphere by turbulent diffusion, which is governed by micro-meteorological conditions (radiation, temperature, wind, etc.) and the roughness of the vegetation, 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 CO₂ 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) and consequently on its effects.

Once ozone has passed the stomatal pore the ozone molecule as a strong oxidant reacts with the apoplastic fluid and this results in the generation of reactive oxygen species (ROS) like the hydroxyl radical ($\cdot\text{OH}$) and the superoxide radical ($\cdot\text{O}_2^-$). These breakdown products of ozone impact on the cell membrane structure and function, change the cell metabolism and cellular events, which results in reduced photosynthetic rates and finally in the generation of observable plant responses like visible 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).

The accumulation of ROS induces defence reactions by the plant that are similar to other oxidative stress responses or pathogen attack and may result in a programmed cell death ("hypersensitive response"), a process which is thought to have the biological significance of limiting the spreading of the oxidative burst (BARTOLI et al., 2013; KANGASJÄRVI et al., 2005; LANGEBARTELS et al., 2002; WOHLGEMUTH et al., 2002). Defence mechanisms involved in detoxifying ROS, directly or indirectly derived from ozone exposure, may consist in enzymatic and non-enzymatic reactions among which the apoplastic ascorbate pool seems to be particularly important (FUHRER, 2009; IRITI and FAORO, 2008). Defence reactions require energy for regeneration of antioxidants, i.e. particularly at prolonged ozone exposure the detoxification capacity may decline due to decreased rates of carbon assimilation and limited available energy (WIESER and MATYSSEK, 2007).

Visible injury resulting from cellular ozone impacts has been observed on a wide range of plant species including trees, crops, and species of semi-natural vegetation, e.g. in North-America and in Europe (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.

Under prolonged, i.e. chronic ozone exposure, visible injury is often not observed, but decreased rates of photosynthesis indicate adverse effects of ozone. The response of photosynthesis to ozone has received

much attention in order to explain ozone induced losses of plant productivity. 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 CO₂ assimilation at the leaf level. However, in trees within-tree alterations of carbon allocation due to disturbed phytohormonal regulation have also been shown to affect growth (KITAO et al., 2012; WINWOOD et al., 2007). 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. Reduced photosynthesis due to ozone exposure may finally result in decreased growth rates and reduced overall plant productivity. Along with these effects impaired translocation of assimilates from source (e.g. leaves) to sink (e.g. roots; seeds) organs and early senescence likely contribute to ozone effects on plant growth and reproduction.

In the past four decades ozone effects on crops (reviewed by e.g. BOOKER et al., 2009; FISCUS et al., 2005; HEAGLE, 1989; HEAGLE et al., 1989; MILLS and HARMENS, 2011) and particularly on deciduous and coniferous trees (reviewed e.g. MATYSSEK et al., 2013; 2010A; 2010B; PERCY et al., 2003; SANDERMANN et al., 1997) have been investigated. Other types of natural or semi-natural vegetation have only recently received attention (reviewed by e.g. ASHMORE, 2005; DAVISON and BARNES, 1998; FUHRER, 1997; WEIGEL et al., 2015).

Very few studies have addressed ozone effects on other organisms than vascular plants (mosses, ferns, algae) in terrestrial ecosystems. Some studies investigated the respiratory and thermoregulatory behaviour of ozone-exposed vertebrates, namely of amphibians and reptiles. Other vertebrate species have only been investigated as test objects in medical research studies and are not considered here.

5 The literature database of the present study

A literature search was performed using WEB OF SCIENCE™ (Core Collection, biological abstracts, and CAB Abstracts) encompassing reviewed papers, book chapters, research reports, or conference proceedings starting with the year 1980 and describing results of controlled exposure of organisms to ozone with at least two different levels of ozone. For vascular plants, which represent the predominant majority of studies, exclusively studies with single plants or monocultures which had been performed in either outdoor ozone exposure facilities (free-air fumigation systems; open-top chambers) or in greenhouses or solardomes were included. Controlled environment studies in growth chambers were considered only, if hourly ozone exposure concentration did not exceed 100 ppb (exceptions are indicated). Ozone effects considered were yield effects (crops only) or general growth effects (i.e. reduction or increase in shoot, foliage, single leaf biomass, stem, root, seed and flower biomass, no. of flowers), change of root/shoot ratio, enhancement and delay of flowering, reduction in germination rate of produced seeds or symptoms of visible leaf/needle injury (unspecific symptoms, senescence, colouring, and ozone specific symptoms). A total of 418 literature references were evaluated which met these requirements. In addition, further 56 publications from forest health monitoring programs were evaluated to identify native plant species, which have been recognised as ozone-sensitive in terms of the expression of ozone-specific symptoms in the field. All data were compiled into a database separated into seven parts. These Source data can be downloaded at <https://www.thuenen.de/en/bd/fields-of-activity/biodiversity-and-climate-change/phytotoxicology-of-air-pollutants/>. Unless otherwise stated, ozone effects were considered as either "none", "statistically significant" or "not significant" as taken from the original publication. For plants native to Germany, further taxonomical information and spatial distribution is given according to BfN (Bundesamt für Naturschutz; <http://www.floraweb.de/index.html>).

6 Identifying ozone sensitive taxa from experimental studies

In the following text the description of the ozone sensitivity of organisms is grouped according to their taxonomy (vascular plants, bryophytes/pteridophytes, algae, lichens, fungi and vertebrates). Ozone effects on microorganisms and invertebrates mostly result from ozone effects on the plant or plant community, respectively, interacting with these organisms. For this reason, these groups of organisms are disregarded here. The large number of studies with vascular plants was further grouped into natural/semi-natural vegetation and crop plants. (Semi)natural vegetation comprises herbaceous and woody plant species including both native wild plants, extensively managed pasture plants and forest trees.

6.1 Native herbaceous and pasture plants

Results from the database

During the last decades an increasing number of experimental studies have been performed to assess the relative sensitivity of natural or semi-natural herbaceous plant species to ozone. In Tab. 1 and Tab. 2 summaries of assessments of ozone responses as indicated by visible symptoms and growth effects of native herbaceous and pasture plant species are shown. Overall, 62 publications were reviewed reporting on either only one or on up to 44 different species. From these publications a number of 554 indications (i.e. entries in the database) were collected which provide information about 298 species belonging to 47 plant families. For 56 species more than two studies are available and 169 species were tested only once. In the majority of studies (documented by 37 publications) open-top chambers or solardomes were used as ozone exposure facilities, however, for 74 species the only available data result from experiments using controlled environment fumigation chambers. About 60% of the species tested were perennials and 20% of all species were grasses.

In total, for 188 species out of the 298 species investigated a response to ozone has been documented. Across the whole data set of herbaceous non-crop plants 53% and 47.5% of all species tested were found to express visible injury symptoms and changes in biomass production, respectively, in at least one experiment. In terms of growth effects (Tab. 2) the proportion of ozone sensitive species is

higher for herbs than for grasses, however, the number of herb species which were tested for their ozone responses is 3.3 times higher than the number of grasses.

A noticeable difference becomes obvious with respect to life history: regarding the parameter visible leaf injury (Tab. 1), the proportion of ozone sensitive species is lower for annuals and biennials as compared to perennials, but the proportion of species responding with ozone impacts on growth (Tab. 2) is higher for annuals and biennials than for perennials. The observation that about one half of the species tested responded to ozone in a sensitive way is also true for species native to Germany including neophytes and archaeophytes (Tab. 1).

In Tab. 3 recorded ozone responses of species are grouped according to the respective plant families. There were six families which were represented by at least ten different species. In terms of visible leaf injuries, six frequently studied families covered more than 50% of species classified to be ozone sensitive for which the following order of decreasing sensitivity could be derived from the dataset: Onagraceae > Fabaceae > Cyperaceae > Lamiaceae > Asteraceae > Poaceae. Considering growth effects, 70% of the species of the Fabaceae tested for their ozone sensitivity were impaired by ozone and about 40% of all species tested to be sensitive towards ozone belong to the families Polygonaceae, Poaceae, Asteraceae, Lamiaceae, and Plantaginaceae. These results for both parameters point to the fact that Fabaceae (legumes) seem to be highly ozone sensitive and that a high proportion of members of Poaceae and Asteraceae families are also sensitive to ozone. On the other hand, for Brassicaceae (crucifers) eight of nine species tested so far proved to be insensitive to ozone exposures.

About one half of all native herbaceous species listed in the present database are also native to Germany, 15 of these species are considered to be “endangered” and additional 12 species are classified as “near-threatened”. Out of these, 16 species (eight within each classification group) are responsive to ozone (Tab. 4). Special attention should be paid to the species *Comarum palustre*, *Medicago minima*, *Nardus stricta* and *Trifolium striatum* because for these species ozone impacts have been shown for both, growth and leaf injury.

Tab. 1: Summary of assessments of ozone effects on native herbaceous or pasture plant species as indicated by visible leaf injury symptoms. Results are classified into different descriptive groups and given as the numbers of total species tested and the numbers of species showing a particular ozone response: spec. = specific ozone symptoms; col. = non-specific discolouration; sen. = symptoms of senescence; not spec. = symptoms not characterized; none = no visible symptoms observed. The percentage of species which were injured to ozone at least in one study is also shown.

descriptive group	no. of species						% injured
	tested	kind of visible symptoms					
		spec.	col.	sen.	not spec.	none	
total	276	28	4	28	112	164	52.9
herbs	211	23	4	16	86	122	51.7
grasses	58	3	0	10	25	40	55.2
sedges	11	2	0	2	1	2	45.5
annuals or biennials	100	4	0	8	34	65	42.0
perennials	175	23	4	20	77	99	58.9
species native to Germany ¹	195	27	4	28	79	120	56.9
endangered ¹	13	0	0	0	3	10	23.1
near threatened ¹	12	5	1	1	2	8	58.3

¹according to Bundesamt für Naturschutz. Floraweb: <http://www.floraweb.de/index.html>.

Sum of responsive and non-responsive species numbers is not equivalent to the total number of species assessed because of divergent results within different publications.

Tab. 2: Summary of assessments of ozone effects on native herbaceous or pasture plant species as indicated by growth effects (change in biomass of shoot, foliage, stem, root, seed or flowers, root/shoot ratio or change in germination rate of produced seeds = seed quality). Results are classified into different descriptive groups and given as the numbers of total species tested and the numbers of species showing a particular ozone response. The percentage of species which were responsive to ozone at least in one study is also shown. Significant changes (see Chapt. 5) are given in parentheses.

descriptive group	no. of species				% responsive
	tested	kind of growth response			
		reduced growth or seed quality	increased growth	none	
total	223	119 (95)	24 (11)	135	61.0 (47.5)
herbs	155	89 (69)	15 (7)	87	63.9 (47.7)
grasses	61	30 (24)	7 (4)	44	55.7 (45.9)
sedges	7	2 (2)	1 (0)	4	42.9 (28.6)
annuals or biennials	55	32 (25)	4 (2)	30	63.6 (49.1)
perennials	166	83 (67)	20 (9)	105	59.0 (44.6)
species native to Germany ¹	187	97 (76)	22 (10)	124	59.9 (44.9)
endangered ¹	12	5 (5)	2 (1)	6	58.3 (50.0)
near threatened	12	3 (2)	0 (0)	12	25.0 (16.7)

¹according to Bundesamt für Naturschutz. Floraweb: <http://www.floraweb.de/index.html>.

Sum of responsive and non-responsive species numbers is not equivalent to the total number of species assessed because of divergent results within different publications.

Tab. 3: Summary of assessments of ozone effects on native herbaceous or pasture plant species categorized according to the respective plant families. The total number of species tested (total) and the number of species showing a response to ozone indicated by visible symptoms and growth effects (see Tab. 1 and Tab. 2) are shown. Statistically significant effects (see Chap. 5) are shown in parentheses. Only those families are considered which are represented by at least three different species.

family	total	visible leaf injuries			growth effects			
		tested	injured	not injured	tested	reduction total (sign.)	increase total (sign.)	not responsive
Apiaceae	4	3	3	0	3	2 (2)	0 (0)	1
Apocynaceae	4	4	4	4	1	1 (1)	0 (0)	0
Asteraceae	59	54	30	26	41	22 (14)	4 (2)	25
Boraginaceae	12	12	4	8	2	2 (1)	0 (0)	0
Brassicaceae	9	9	1	8	2	2 (2)	0 (0)	1
Caryophyllaceae	10	8	1	8	10	5 (4)	2 (2)	8
Cyperaceae	10	9	7	2	10	3 (3)	1 (0)	6
Fabaceae	29	28	22	7	25	20 (16)	1 (0)	6
Geraniaceae	3	3	2	2	1	0	0	2
Hyperaceae	3	3	2	2	2	1 (0)	0	1
Lamiaceae	9	9	5	5	5	2 (2)	2 (1)	3
Malvaceae	3	3	2	1	3	2(1)	0	1
Onagraceae	8	8	8	4	2	2 (2)	0	1
Papaveraceae	5	5	2	3	3	2 (2)	0	2
Plantaginaceae	7	7	2	7	6	3(1)	1 (0)	5
Poaceae	64	55	30	39	58	29 (23)	7 (4)	42
Polemoniaceae	3	3	0	3	0	n.d.	n.d.	n.d.
Polygonaceae	9	8	5	5	6	5 (5)	1 (1)	3
Ranunculaceae	4	4	2	3	3	1 (1)	0	3
Rosaceae	7	6	3	5	7	4 (4)	2 (0)	3
Saxifragaceae	3	3	0	3	3	0	0	3
Scrophulariaceae	4	4	1	3	3	3 (3)	0	2
Violaceae	3	3	1	2	3	1 (1)	0	2

Tab. 4: Vascular plant species at risk (species red list) which have been tested for their response to ozone with respect to visible injuries and growth effects. If distinct effects have been published, the most sensitive one is listed. red. = reduction, inc. = increase, n.s. = not significant, -- = not determined. Risk status according to "Bundesamt für Naturschutz": NT – near threatened, 3: vulnerable, 2: endangered, 1: critically endangered, 0: extinct in the wild, R: extremely rare

<i>species</i>	<i>status</i>	<i>visible injury</i>	<i>growth effect</i>	<i>reference</i> ¹
<i>Antennaria dioica</i>	3+	--	shoot red.	MORTENSEN, 1993
<i>Avenula pratensis</i>	NT	no	no	ASHMORE et al., 1996
<i>Briza media</i>	NT	no	no	ASHMORE et al., 1996; 1995
<i>Carex laevigata</i>	3	no	no	HAYES et al., 2006
<i>Carex panicea</i>	NT	specific	no	HAYES et al., 2006
<i>Carum carvi</i>	NT	specific	no	BUNGENER et al., 1999B
<i>Cirsium dissectum</i>	2	no	shoot red., n.s.	FRANZARING et al., 2003; 2000
<i>Coramrum palustre</i>	NT	yes	growth red.	MORTENSEN, 1994
<i>Eriophorum vaginatum</i>	NT	--	no	MORSKY et al., 2011
<i>Gentiana asclepiadea</i>	3	yes	--	MANNING and GODZIK, 2004
<i>Juncus squarrosus</i>	NT	no	inc. in growth	HAYES et al., 2006
<i>Lychnis flos-cuculi</i>	NT	coloured/ specific	no	BUNGENER et al.; 1999b; BATTY et al., 2001; FRANZARING et al., 2000; TONNEJCK et al., 2004
<i>Lychnis viscaria</i>	NT	no	no	BATTY et al., 2001
<i>Medicago minima</i>	3	yes	growth red.	GIMENO et al., 2004
<i>Micropyrum tenellum</i>	0	no	--	BERMEJO et al., 2003
<i>Nardus stricta</i>	NT	specific	shoot red.	ASHMORE et al., 1996; HAYES et al., 2006
<i>Narthecium ossifragum</i>	3	no	no	HAYES et al., 2006
<i>Primula farinosa</i>	3+	no	no	BATTY et al., 2001
<i>Rhodiola rosea</i>	R	--	no	BATTY et al., 2001
<i>Rubus chamaemorus</i>	1	no	--	MORTENSEN AND NILSEN, 1992
<i>Salvia pratensis</i>	NT	senescent	no	BUNGENER et al., 1999a; 1999b
<i>Saussurea alpina</i>	R	--	inc. in growth.	MORTENSEN, 1993
<i>Scrophularia auriculata</i>	3	no	growth red.	BATTY et al., 2001
<i>Senecio sarracenicus</i>	3	no	inc. in shoot	HAYES et al., 2006
<i>Silene noctiflora</i>	NT	no	no	BATTY et al., 2001
<i>Succisa pratensis</i>	NT	--	no	FRANZARING et al., 2000
<i>Tragopogon orientalis</i>	NT	specific	no	BUNGENER et al., 1999a; 1999b
<i>Trifolium striatum</i>	3	yes	shoot / seed red.	BERMEJO et al., 2003; GIMENO et al., 2004; SANZ et al., 2007

¹⁾ ASHMORE, M.R., POWER, S.A., COUSINS, D.A., AINSWORTH, N., 1996: In: L. KÄRENLAMP, L. SKÄRBY (eds.), Critical Levels for Ozone: UN-ECE Workshop Report, Kuopio, 193-197. ²⁾ ASHMORE, M.R., THWAITES, R.H., AINSWORTH, N., 1995: Water Air Soil Pollut 85, 1527-1532; BATTY, K., ASHMORE, M., POWER, S.A., 2001: In: D. FOWLER et al. (eds.), The Ozone Umbrella Project CEH Project: C00970 – Final Report, Centre for Ecology and Hydrology, Edinburgh; BERMEJO, V., GIMENO, B.S., SANZ, J., DE LA TORRE, D., GIL, J.M., 2003: Atmos. Environ. 37, 4667-4677; BUNGENER, P., BALLS, G.R., NUSSBAUM, S., GEISSMANN, M., GRUB, A., FUHRER, J., 1999A: New Phytol. 142, 271-282; BUNGENER, P., NUSSBAUM, S., GRUB, A., FUHRER, J., 1999b: New Phytol. 142, 283-293; FRANZARING, J., DUECK, T.A., TONNEJCK, A.E.G., 2003: In: P.E. KARLSSON, G. SELLDÉN, H. PLEJEL (eds.), Establishing Ozone Critical Levels II, UNECE Workshop report B 1523. IVL Swedish Environmental Research Institute, Gothenburg, Sweden, 224-229; FRANZARING, J., TONNEJCK, A.E.G., KOOLMAN, A.W.N., DUECK, T.A., 2000: Environ. Exp. Bot. 44, 39-48; GIMENO, B.S., BERMEJO, V., SANZ, J., DE LA TORRE, D., ELVIRA, S., 2004: Environ. Pollut. 132, 297-306; HAYES, F., MILLS, G., WILLIAMS, P., HARMENS, H., BUKER, P., 2006: Atmos. Environ. 40, 4088-4097; MANNING, W.J., GODZIK, B., 2004: Environ. Pollut. 130, 33-39; MORSKY, S.K., HAAPALA, J.K., RINNAN, R., SAARNIO, S., SILVOLA, J. et al., 2011: Environ. Exp. Bot. 72, 455-463; MORTENSEN, L.M., 1993: Norweg. J. Agric. Sci. 7, 129-138; MORTENSEN, L.M., 1994: Norweg. J. Agric. Sci. 8, 91-97; MORTENSEN, L.M., NILSEN, J., 1992: Norweg. J. Agric. Sci. 6, 195-204; SANZ, J., BERMEJO, V., GIMENO, B.S., ELVIRA, S., ALONSO, R., 2007: Atmos. Environ. 41, 8952-8962; TONNEJCK, A.E.G., FRANZARING, J., BROUWER, G., METSSELAAR, K., DUECK, T.A., 2004: Environ. Pollut. 131, 205-213.

Literature context: Approaches to describe functional patterns of plant responses to ozone

During the last decades an increasing number of experimental studies have been performed to assess the relative sensitivity of natural or semi-natural herbaceous plant species to ozone. The majority

of these studies focused on highland or alpine (BUNGENER et al., 1999A; BUNGENER et al., 1999B), dehesa (GIMENO et al., 2004), wetland (BATTY et al., 2001; FRANZARING et al., 2003; FRANZARING et al., 2000) or ruderal plant species (BENDER et al., 2006; BERGMANN et al., 1999), and in most of the studies rare species were included

as well. Beyond the repeated documentation of widespread ozone sensitivity of native herbaceous species it is impossible to assess the ozone risk of the total flora only by doing standardised screening experiments. Therefore, several functional approaches have been described in order to identify ecological characteristics which might be associated with the sensitivity of the native herbaceous plants to ozone. Relating eco-physiological characteristics to ozone sensitivity of different species, HARKOV and 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 by ozone than scleromorphous species adapted to dry sites. However, the authors failed to evidence a relationship between ozone sensitivity ranking and ELLENBERG-moisture values, especially when the assessment was based on growth parameters. In open-top chamber 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 are therefore considered to be particularly sensitive because of a higher stomatal conductance. In both studies, 36% of the species responded with growth changes and 56% expressed symptoms of leaf injury. This reflects a ratio of sensitivity below or similar to that calculated for the whole data set over all habitats as presented in the present study. Moreover, there was no association between ecological indicator values for either moisture, light, pH and fertility or ozone sensitivity in the short-term experiments of BATTY et al. (2001). However, the most sensitive species in the experiments were characterised by a high stomatal conductance.

From a meta-analysis HAYES et al. (2007) identified three significant relationships between relative sensitivity to ozone and ecological habitat requirements, i.e. light, moisture and salt content of soils. These relationships provided an opportunity to model the relative sensitivity to ozone of species (JONES et al., 2010). In a review of ozone impacts on European grasslands BASSIN et al. (2007) pointed out that stomatal conductance, specific leaf area (SLA) and defense capacity are three main plant traits that determine ozone sensitivity. Low relative growth rate (RGR) and SLA are characteristic for stress tolerating species (S-strategy sensu the C-S-R strategy model of GRIME (1979), but there is limited evidence that these species are less sensitive towards ozone than species with the highest ranking of C (competitive)- or R (ruderal)-strategy (BASSIN et al., 2007; BUNGENER et al., 1999; FRANZARING et al., 1997; HAYES et al., 2007).

However, a basic requirement for deriving any kind of relationship between a 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 are not sufficiently represented in the databases of experiments under realistic conditions (BASSIN et al., 2007; HAYES et al., 2007) narrowing the success in grouping the plant kingdom into broad classes of ozone sensitivity. HAYES et al. (2007) determined an index to describe the relative sensitivity to ozone for 83 native plant species from existing publications. Approximately one-third of the species in this study showed above-ground biomass reductions of about > 10% under ozone exposure. The authors concluded that plants of the Fabaceae family and species with a therophyte life form have to be regarded as particularly sensitive to ozone. The ranking of species in this study derived from ozone dose-response relationships and was related to a standardized ozone exposure and is thus of high confidence. Nevertheless, the main observations of this study comply with our findings when the data set for the 298 species shown Tab. 2 and Tab. 3 is regarded. 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 of species associated with grasslands (MILLS et al., 2007). 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. (2007) 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. With respect to the present study these results can only be confirmed for the occurrence of growth effects but not for visible ozone injuries.

6.2 Woody plants

Results from the data base

This chapter summarizes existing information on the ozone sensitivity of woody plants species based on their responses with respect to visible symptoms (Tab. 5) or growth effects (Tab. 6) as well as their classification to plant families (Tab. 7). The data set contains results taken out of a total of 142 references, with 56 originating from America, 16 from Asia and 67 from Europe. In summary, a total of 360 entries covering 165 species, 69 genera and 39 families have been found within the references selected. About two third of the species listed are categorised as trees, the rest are shrubs or climbers and an equal proportion as deciduous in contrast to evergreen species. With respect to the German situation 39 species that were described in ozone exposure studies are native to Germany, and 28 species are neophytes. *Populus nigra* was the only species classified as endangered in Germany. The majority of results (92 studies) was achieved using open top chambers as an ozone exposure system while only 13 studies used free-air fumigation facilities. Only six studies presented here investigated mature trees of the species European larch (HAVRANEK and WIESER, 1993), red oak (KELTING et al., 1995; SAMUELSON et al., 1996), Scots pine (MANNINEN et al., 2003), beech (NUNN et al., 2005), and apple (WILTSHIRE et al., 1993) whereas all other investigations are based on experiments with cuttings or seedlings (one to eight years old). However, while more recently there is a number of ozone exposure studies working with mature trees, these studies focussed on eco-physiological issues, which are not considered here.

About 64% of all woody species (105 species) were investigated in only one study and 18% and 20%, respectively, in two or more studies. The most frequently studied species were *Liriodendron tulipifera*, *Viburnum lantana*, *Acer saccharum*, *Pinus sylvestris*, *Populus deltoides* × *nigra*, *Prunus serotina*, *Quercus rubra*, and *Betula pendula* (6 to 10 times) and *Pinus taeda*, *Fraxinus excelsior*, *Fagus sylvatica*, and *Picea abies* (> 10 times).

A total of 148 species was shown to be responsive to ozone. In terms of visible leaf injuries more than 80% of 135 species tested expressed symptoms when exposed to ozone. This percentage is slightly higher for deciduous and broadleaved species than for evergreen or coniferous species. About one half of all observations, which represent 62.6% of the species, revealed significant growth responses to ozone. Differences in the ozone sensitivity between coniferous and broadleaved species are minimal with a slight tendency to more sensitive responses of deciduous versus evergreen species. In general, there is no evidence of a significant increase in growth due to an ozone exposure. Similar to native herbaceous species (Chap. 6.1), a higher percentage of responsive species was detected when assessing visible

leaf injury rather than growth measurements. However, the averaged percentage of ozone responsive woody species is higher than that of herbaceous species (see Tab. 1 and Tab. 2). For 64 species both parameters, visible injury and growth, have been investigated simultaneously. For a majority of more than 70% (46 species) concordant results were recorded i.e. an impact of ozone was evidenced by both, visible injury and growth effects.

Tab. 7 summarizes the ozone responses of species according to the respective plant families. The family of the Pinaceae was represented by the highest number of species (28) followed by the families of Salicaceae, Rosaceae, Fagaceae, and Caprifoliaceae. These 5 frequently studied families cover 54% of all species tested and involve about one third of species shown to be responsive to ozone.

Tab. 5: Summary of assessments of ozone effects on woody plant species indicated by visible leaf injury symptoms. Results are classified into different descriptive groups and given as the numbers of species tested and the number of species showing a particular ozone response. The percentage of species which were responsive to ozone at least in one study is also shown.

descriptive group	no. of species			% injured
	tested	injured	not injured	
total	135	114	39	84.4
shrubs	33	28	8	84.8
trees	84	70	23	83.3
climbers	3	2	1	--
deciduous	90	78	23	86.7
evergreen	41	31	16	75.6
conifers	18	13	9	72.2
broadleaved	118	101	30	85.6
native to Germany ¹	63	59	17	93.7

¹ according to Bundesamt für Naturschutz. Floraweb: <http://www.floraweb.de/index.html>

Tab. 6: Summary of assessments of ozone effects on woody plant species indicated by growth effects (change of total plant or organ biomass). Results are classified into different descriptive groups and given as the numbers of species tested and the number of species showing a particular ozone response. Statistically significant effects (see Chap. 5) are shown in parentheses. The percentage of species which were responsive to ozone at least in one study is also shown; none = no ozone effects observed.

descriptive group	no. of species				% responsive total (sign.)
	tested	decreased growth total (sign.)	increased growth total (sign.)	none	
total	99	76 (62)	2 (0)	54	76.8 (62.6)
shrubs	3	2 (2)	0	2	--
trees	89	71 (56)	2 (0)	37	79.8 (62.9)
climbers	1	1 (1)	0	0	--
deciduous	51	41 (33)	2 (0)	19	80.4 (64.7)
evergreen	48	34 (28)	0	23	70.8 (58.3)
conifers	30	19 (16)	0	17	63.3 (53.3)
broadleaved	69	57 (46)	2 (0)	25	82.6 (66.7)
native to Germany ¹	36	28 (22)	2 (0)	20	77.8 (61.1)

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.

¹ according to Bundesamt für Naturschutz. Floraweb: <http://www.floraweb.de/index.html>

Irrespective of the kind of ozone response (i.e. visible injuries or growth effects) the families Myrtaceae, Oleaceae, Salicaceae, and Betulaceae comprise the highest proportion of responsive species, followed by Fagaceae, Sapindaceae, Rosaceae, and Pinaceae. However, because of the general high proportion of responsive species the differences between the plant families are quite small. For example, out of the most frequently investigated family of the Pinaceae, which are classified here to be less sensitive to ozone, 72% of the species were found to express visible symptoms and 52% showed significant growth effects at least in one investigation.

Literature context: Approaches to evaluate the sensitivities of species to ozone based on ecophysiological parameters

The data listed in the present study clearly reflect the fact that our available knowledge about the ozone sensitivity of trees and shrubs derives predominantly from potted juvenile individuals. Accordingly, KARNOSKY et al. (2007) pointed out that during more than 50 years of research negative growth effects on forest trees have been demonstrated mainly for 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 and 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 mature trees some attempts to investigate ozone effects were made by the use of branch cuvettes (WIESER et al., 2012), while the free-air ozone exposure system established in Germany in a mixed stand of about 60-year-old *Fagus sylvatica* and *Picea abies* trees (NUNN et al., 2002) remains unique.

Nevertheless, research activities on ozone effects on woody plant species performed within the last decades revealed a broad knowledge about visible symptoms, effects on growth, carbohydrate allocation, ozone detoxification and to a high extent about effects of

Tab. 7: Summary of assessments of ozone effects on woody plant species categorized according to the respective plant families. The total number of species tested (total) and the number of species showing a response to ozone indicated by visible symptoms and growth effects (Tab. 5 and Tab. 6) are shown. Statistically significant effects (see Chap. 5) are shown in parentheses. Only those families are considered which are represented by at least three different species.

family	total	visible leaf injuries			growth effects		
		tested	injured	not injured	tested	responsive total (sign.)	not responsive
Anacardiaceae	3	3	3	1	0	0 (0)	0
Betulaceae	8	6	5	2	6	5 (5)	2
Caprifoliaceae	11	11	8	5	0	0 (0)	0
Cornaceae	3	3	3	1	0	0 (0)	0
Cupressaceae	3	0	0	0	3	2 (2)	1
Fabaceae	3	2	1	2	2	2 (1)	0
Fagaceae	14	9	8	3	10	8 (7)	5
Lauraceae	3	2	1	1	2	2 (2)	1
Myrtaceae	9	9	8	1	8	8 (8)	1
Oleaceae	5	5	5	1	4	4 (2)	1
Pinaceae	28	18	13	9	27	17 (14)	16
Rosaceae	16	14	12	4	11	9 (5)	4
Salicaceae	20	16	15	2	9	9 (7)	3
Sapindaceae	8	7	6	3	4	3 (2)	0
Tiliaceae	3	3	2	1	0	0 (0)	0

ozone on photosynthesis and stomatal functioning (e.g. reviewed by GOMEZ-GARAY et al., 2013; PAOLETTI, 2007). These measurements suggested that ozone reduces stomatal conductance and may impair stomatal control and predispose trees to drought stress under dynamic conditions. 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 biodiversity issues the knowledge about different ozone sensitivity of species is important. For example, based on the 38 experiments reviewed by HUTTUNEN and 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 uptake 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 and GEROSA, 2002). Similarly, the present analysis revealed a slight trend of higher ozone tolerance for evergreen or coniferous species (Tab. 5 and Tab. 6).

6.3 Agricultural and horticultural crops

Results from the data base

In total 478 entries were found in 195 literature references that meet the above mentioned requirements for the experimental setup and comprise information on the response to ozone of 54 crop species. With very few exceptions, the cultivars of these species tested are exactly specified, so that in total data are available for 350 different genotypes (Tab. 8). More than half of the studies were performed using open-top chambers as exposure systems. Recently data for *Glycine max*, *Oryza sativa*, *Phaseolus vulgaris*, *Solanum tuberosum*, and *Triticum aestivum* are also available from free-air fumigation systems. The majority of data contained in the database derived from European studies but due to a growing awareness of air pollution impacts in China and India for example, a high number of data derived from more recently published Asian studies.

Different from the other plant groups, testing of agricultural and horticultural crop plants for their ozone sensitivity has started already in the 1950s in the USA. Moreover, as these studies were always related to the commercial use of agricultural and horticultural crop species they nearly always comprised one or several clearly defined cultivars of a species. Implicitly, the use of such cultivars also resembled the result of breeding activities which intended to optimize a cultivar to its particular environment including ozone pollution (see below). Thus the studies referred to in the present investigation (not before 1980) have been performed when the sensitivity of many crop species and cultivars, respectively, was already known. Apart from some new 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 (Tab. 8).

Out of the 55 species considered here 17 have only been investigated in one study which for example comprises six ancestors of modern wheat cultivars. Generally, wheat was the most frequently studied species, followed by bean, rice and soybean (Tab. 9), each represented by 29 to 49 different cultivars. According to the present data 75 %

Tab. 8: Summary of information on growth and visible injury effects of ozone on agricultural and horticultural crops. Numbers of records (entries in the database), species, and cultivars or genotypes investigated described in 195 relevant publications including the relative share of responses to ozone.

	tested (no.)			responsive (%)		
	visible injury	growth	both	visible injury	growth	both
records	214	413	150	88.3	80.9	80.0
species [#]	48	47	35	89.6	91.5	91.4
cultivars/genotypes*	179	308	127	88.3	82.8	80.3

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

Tab. 9: Summary of the ozone sensitivity of 55 agricultural and horticultural crop species. Data refer to the number of cultivars of each species and are shown as the number of responsive cultivars in relation to the total number of cultivars investigated.

species	responsive	total	species	responsive	total
<i>Aegilops tauschii</i>	1	1	<i>Medicago sativa</i>	5	5
<i>Allium ampeloprasum</i>	0	1	<i>Nicotiana tabacum</i>	7	9
<i>Allium cepa</i>	5	5	<i>Oryza sativa</i>	31	47
<i>Arachis hypogaea</i>	1	1	<i>Phaseolus vulgaris</i>	39	42
<i>Avena sativa</i>	0	1	<i>Pisum sativum</i>	1	1
<i>Beta vulgaris</i>	2	2	<i>Raphanus sativus</i>	3	4
<i>Brassica campestris</i>	10	10	<i>Saccharum spp.</i>	1	1
<i>Brassica juncea</i>	2	2	<i>Solanum lycopersicum</i>	10	11
<i>Brassica napus</i>	2	2	<i>Solanum tuberosum</i>	7	7
<i>Brassica napus ssp. oleifera</i>	1	5	<i>Spinacia oleracea</i>	1	?
<i>Brassica oleracea</i>	2	5	<i>Trifolium alexandrinum</i>	6	6
<i>Brassica rapa</i>	4	4	<i>Trifolium repens</i>	5	5
<i>Cicer arietinum</i>	2	2	<i>Trigonella foenum-graecum</i>	1	1
<i>Citrullus lanatus</i>	7	7	<i>Triticosecale wittmack</i>	1	1
<i>Corchorus olitorius</i>	1	1	<i>Triticum aestivum</i>	50	50
<i>Coriandrum sativum</i>	1	1	<i>Triticum boeoticum</i>	1	1
<i>Cucumis melo</i>	2	2	<i>Triticum dicoccum</i>	1	1
<i>Cucurbita pepo</i>	1	3	<i>Triticum durum</i>	11	11
<i>Daucus carota</i>	2	2	<i>Triticum monococcum</i>	1	1
<i>Eruca sativa</i>	2	2	<i>Triticum polonicum</i>	1	1
<i>Fragaria × ananassa</i>	4	4	<i>Triticum timopheevii</i>	1	1
<i>Glycine max</i>	27	28	<i>Valerianella locusta</i>	1	1
<i>Gossypium barbadense</i>	1	4	<i>Vicia faba</i>	0	1
<i>Gossypium hirsutum</i>	8	8	<i>Vigna mungo</i>	1	1
<i>Hordeum vulgare</i>	3	8	<i>Vigna radiata</i>	7	7
<i>Lactuca sativa</i>	9	11	<i>Vigna unguiculata</i>	2	2
<i>Linum usitatissimum</i>	2	2	<i>Zea mays</i>	6	6
<i>Lycopersicon pimpinellifolium</i>	1	1			

of all cultivars were studied only once, 15.2% (52 cvs) twice and only 6.4% (22 cvs) three times. Cultivars investigated repeatedly (more than three experimental studies) were *Lactuca sativa* cv. Paris Island (4×), *Triticum aestivum* cv. Turbo, *Oryza sativa* cv. Koshihikari, and *Solanum tuberosum* cv. Bintje (5×), *Glycine max* cv. Essex (7×) and *Phaseolus vulgaris* cv. Lit (8×).

Although about 90% of all experiments proved an ozone sensitive response of the considered cultivar, for the following cultivars di-

vergent responses to ozone were observed in different studies: *Brassica campestris* cv. Wisconsin Fast Plants, *Fragaria × 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 (growth), *Solanum lycopersicum* cv. Pusa Ruby, *Phaseolus vul-*

garis cv. Bush Blue Lake 274, and *Triticum aestivum* cv. Riband (injury).

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 database comprises 465 entries and put emphasis on cultivar comparisons. Referred to the literature considered, 82 studies met these requirements. A total for 29 species have been investigated comparatively within one experiment, in which the number of cultivars per study ranged from 2 to 20 (*Oryza sativa*). The species, which most frequently were subjected to cultivar comparisons or screenings were *Glycine max*, *Nicotiana tabacum*, *Oryza sativa*, *Phaseolus vulgaris*, and *Triticum aestivum*. For the following 22 species no comparative studies were found: *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*, and *Valerianella locusta*

Literature context: Importance of breeding activities

In order to maintain the productivity of agricultural and horticultural crops in a high ozone environment the development and use of ozone insensitive/tolerant cultivars is suggested to be the most economical and practical solution (AVNERI et al., 2013; BISWAS et al., 2009; BURKEY and CARTER, 2009; FOY et al., 1995) and the knowledge about the genetic background of ozone sensitivity/tolerance is fundamental for breeding ozone tolerant cultivars (BISWAS et al., 2008A).

Due to its importance for human nutrition wheat (*Triticum aestivum*) has repeatedly been tested for its ozone sensitivity (83 records, 50 cultivars; Tab. 9). Intraspecific variations of ozone sensitivity of wheat has been found for some modern cultivars (KOU et al., 2012; KOU et al., 2013; REICHENAUER et al., 1998; SARKAR and AGRAWAL, 2010; TIWARI et al., 2005), while in other studies different cultivars responded similarly to ozone (AKHTAR et al., 2010; BARNES et al., 1995; ZHU et al., 2011). A screening study of yields of old and modern cultivars clearly showed that the more modern cultivars exhibited a greater sensitivity to ozone than older cultivars (BARNES et al., 1990; BISWAS et al., 2008A; BISWAS et al., 2008B; VELISSARIOU et al., 1992). It was assumed that selection by plant breeders for higher stomatal conductance and hence, higher CO₂ assimilation, inadvertently led to higher ozone uptake rates in modern cultivars resulting in higher sensitivity to ozone than their predecessors (BARNES et al., 1990; VELISSARIOU et al., 1992). While for wheat this has also been questioned (BISWAS et al., 2009; FENG et al., 2011; INADA et al., 2012), for soybean, however, the same mechanism, i.e. an increasing ozone sensitivity of more modern cultivars, was suggested by OSBORNE et al. (2016). The latter authors analysed 28 experimental studies reporting on 49 soybean cultivars in total and found an increase in ozone sensitivity of soybean by an average of 32.5% between 1960 and 2000 based on the year of cultivar release. Although the underlying mechanisms remain unclear, the fact that ozone sensitivity has been changed due to selection by plant breeders seems to be obvious.

6.4 Mosses and ferns

There were only 9 references which were selected to be appropriate to describe effects of ozone on mosses and ferns. This resulted in 21 records of 14 species (Tab. 10). In these studies exposure to ozone included controlled environment and open-top chamber studies and comprised two fern species (*Athyrium felix-femina* and *Onoclea sensibilis*), 8 species of the *Sphagnum* genus and the two other moss species (*Dicranum polysetum* and *Pleurozium schreberi*). Visible in-

jury was either absent or not determined and reductions in growth or spore germination were observed on two species each (Tab. 10). On the other hand, the species regarded here proved to be highly ozone sensitive when physiological parameters, i.e. membrane permeability or ultrastructure of organelles were considered. However, overall the data basis for these taxa is very small and it remains difficult to assess the sensitivity of mosses and especially of ferns towards ozone in established ecosystems. As outlined by NIEMI (2003) due to their morphological structure, stomatal control does not play a role for ozone uptake into the mosses and the permanent water film covering the leaf surfaces of mosses is thought to act as an ozone scavenger. This argument does not point to a particular ozone risk for these species.

6.5 Algae, lichens, and phyllosphere fungi

Most experimental studies with algae species have been carried out either with *Chlorella sorokiniana* (HEATH, 1984; HEATH et al., 1982; SWANSON et al., 1982) or *Euglena gracilis* (BILODEAU and CHEVRIER, 1998; CHEVRIER et al., 1990; CHEVRIER and SARHAN, 1992; CHEVRIER et al., 1988). In these studies the algae were grown in cell cultures and ozone was injected into the liquid growth medium. All relevant studies refer to investigations on the mechanisms of ozone-induced oxidative damages and repair processes at the cellular level using the algae as model cells. Lichens represent a symbiotic system of fungi and algae. Similar to mosses lichens lack a waterproofing cuticle and stomata, and are thus exposed to ozone directly at their surface cell layers. Lichens are known to be highly responsive to SO₂ (AHN et al., 2011; LACKOVICOVA et al., 2013) and HNO₃ (RIDDELL et al., 2012).

Studies with lichens using experimental ozone exposures are listed in Tab. 11 and comprise mainly controlled environment conditions. In total 31 lichen species have been tested for their ozone sensitivity. With the exception of the observation of visible injuries described by RUOSS and VONARBURG (1995) and SCHEIDEGGER and SCHROETER (1995) physiological and structural impairments have frequently been observed as a result of controlled exposure to high ozone levels. From a study with three lichen species using open-top chambers BERTUZZI et al. (2013) concluded, that lichens may be considered as rather ozone-tolerant organisms.

Lichens were frequently used as bioindicators for photochemical oxidant air pollution e.g. in the USA (MCCUNE, 1988; WILL-WOLF et al., 1996), Scandinavia (OKSANEN et al., 1990; OLSSON, 1995), Switzerland (RUOSS and VONARBURG, 1995), Italy (LORENZINI et al., 2003; NALI et al., 2007), Slovenia (BATIC and KRALJ, 1996), and Korea (AHN et al., 2011; HUR and KIM, 2000). With respect to ozone their suitability as bioindicators for this pollutant was deduced from field observation in the San Bernardino Mountains e.g. (NASH and SIGAL, 1999). However, the lack of a correlation with other ozone response data (BATIC and KRALJ, 1996; LORENZINI et al., 2003) or ozone exposures indices (AHN et al., 2011; NALI et al., 2007; RUOSS and VONARBURG, 1995) led to the conclusion that lichens are not suitable for monitoring ozone episodes.

Few studies have addressed the question if and to what extent fungi respond to an ozone exposure and these studies focused on phyllosphere species. MAGAN et al. (1995) analysed the phyllosphere microbial populations inhabiting the needles surfaces of conifer species in an open-air fumigation experiment. After three years of exposure to ozone they found an increase in the occurrence of *Sclerophoma pythiophila* on *Picea sitchensis* but a decrease of *Epicoccum nigrum* and *Cladosporium* spp. on *Pinus sylvestris*, while the total fungal populations or the fungal biomass was increased on the needles of this species. FENN et al. (1989) examined populations of phyllosphere fungi from leaves of the tree species *Sequoiadendron giganteum* and *Quercus kelloggii* which were exposed to 1.5× of the ambient

Tab. 10: Effects of ozone exposure on moss and fern species. Detailed list of all experimental studies considered. Ozone concentrations (ppb) are given in parentheses. Controlled = controlled environment studies; OTC = open top chambers studies

<i>species</i>	<i>exposure</i>	<i>effect</i>	<i>reference</i>
<i>Athyrium felix-femina</i>	controlled (50, 100, 150)	reduced spore germination	BOSLEY et al. (1998)
<i>Dicranum polysetum</i>	OTC (80)	no injury	NYGAARD (1994)
<i>Hylocomium splendens</i>	OTC (80)	no injury	NYGAARD (1994)
<i>Onoclea sensibilis</i>	controlled (50, 100, 150)	reduced spore germination	BOSLEY et al. (1998)
<i>Pleurozium schreberi</i>	OTC (80)	no injury	NYGAARD (1994)
<i>Polytrichum commune</i>	controlled (50, 100, 150)	none	BOSLEY et al. (1998)
	controlled (50, 100, 150)	no effect on protonematal growth or gametophore production	PETERSEN et al. (1999)
	OTC (70-80)	(reduced growth)	POTTER et al. (1996A)
<i>Sphagnum angustifolium</i>	controlled (50, 100, 150)	decreased cell cross-sectional area occupied by chloroplasts	RINNAN and HOLOPAINEN (2004)
	controlled (50, 100, 150)	increase in membrane permeability	NIEMI et al. (2002)
<i>Sphagnum capillifolium</i>	controlled(50, 100, 1150)	none	POTTER et al. (1996b)
<i>Sphagnum cuspidatum</i>	controlled(50, 100, 1150)	none	POTTER et al. (1996B)
<i>Sphagnum flexuosum</i>	OTC (80)	none	GAGNON and KARNOSKY (1992)
<i>Sphagnum magellanicum</i>	controlled (50, 100, 150)	ultrastructural changes	RINNAN and HOLOPAINEN (2004)
	OTC (80)	reduced chlorophyll concentration	GAGNON and KARNOSKY (1992)
<i>Sphagnum papillosum</i>	controlled (150)	none	POTTER et al. (1996B)
	controlled (50, 100, 150)	cellwall became thinner, decreased chloroplast size	RINNAN and HOLOPAINEN (2004)
	AA	no growth effects	MORSKY et al. (2011)
<i>Sphagnum recurvum</i>	OTC (70-80)	reduced growth	POTTER et al. (1996A)
	controlled (150)	reduction in photosynthesis, increased membrane leakage	POTTER et al. (1996B)
<i>Sphagnum rubellum</i>	OTC (80)	reduced chlorophyll concentration	GAGNON and KARNOSKY (1992)

BOSLEY, A., PETERSEN, R., REBBECK, J., 1998: Bryologist 101, 512-518; GAGNON, Z.E., KARNOSKY, D.F., 1992: J. Bryol. 17, 81-91; MORSKY, S.K., HAAPALA, J.K., RINNAN, R., et al., 2011: Environ. Exp. Bot. 72, 455-463; NIEMI, R., MARTIKAINEN, P.J., SILVOLA, J., HOLOPAINEN, T., 2002: Sci. Total Environ. 289, 1-12; NYGAARD, P.H., 1994: Rapport fra Skogforsk, 1-17; PETERSEN, R.L., BOSLEY, A., REBBECK, J., 1999: Bryologist 102, 398-403; POTTER, L., FOOT, J.P., CAPORN, S.J.M., LEE, J.A., 1996A: New Phytol. 134, 649-656; POTTER, L., FOOT, J.P., CAPORN, S.J.M., LEE J.A., 1996B: J. Bryol. 19, 19-32; RINNAN, R., HOLOPAINEN, T., 2004: Ann. Bot.-London 94, 623-634.

ozone concentration within OTC's 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. Similarly, VON TIEDEMANN et al. (1991) in an OTC study reported on a chamber effect on the saprobial colonization of the phyllosphere of *Triticum aestivum*, while there was no ozone effect.

6.6 Vertebrates

Information on responses of vertebrates to controlled ozone exposures found in the literature mainly refer to ozone exposure studies with laboratory test animal associated with medical (pulmonary) research and are not relevant in the present context. The few existing studies that might be relevant for terrestrial ecology exclusively used acute exposure to high levels of ozone (up to 800 ppb) and are thus also not further described here. Nevertheless, the species tested in these studies included guinea pig (*Cavia porcellus*, SU and GORDON, 1997), toad (*Bufo marinus*, DOHM and MAUTZ, 2001; DOHM et al., 2008; DOHM et al., 2001; JOHNSON et al., 2009), frog and lizard

(*Pseudacris cadaverina* and *Sceloporus occidentalis*, MAUTZ and DOHM, 2004). For these vertebrates species adverse ozone effects on immune function, respiration, and feeding behaviour as well as induced hypothermia are described. No classification of an ozone sensitivity can be derived from these studies.

7 Identifying sensitive taxa from field observations and case studies

In contrast to the previously described experimental studies in the following chapter observations are compiled that describe actual impacts of the prevailing ambient ozone exposure scenario at a particular site or region on constituents of the ecosystem.

With the raising awareness of symptoms of forest damage several national and international monitoring and research programs have been initiated to assess both the extent of ecosystem impacts and their causal agents including ozone. Examples at a national, international and regional scale are the US 'Forest Health Monitoring (FHM)' or the 'International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests)' of the UNECE, the US 'San Bernardino Mountains Network Study (SBM)', the US 'The Vital Signs Program of the U.S. National Park

Tab. 11: Effects of ozone exposure on lichens. Detailed list of all experimental studies considered. Ozone concentrations (ppb) are given in parentheses. Controlled = controlled environment studies; OTC = open top chambers studies

species	exposure	effect	references
<i>Anaptychia ciliaris</i>	controlled (150)	discolored parts	RUOSS and VONARBURG (1995)
	field fumigation (90)	decreased chlorophyll fluorescence, decreased photosynthesis	SCHEIDEGGER and SCHROETER (1995)
	controlled (300)	none	CALATAYUD et al. (2000)
<i>Bryoria capillaris</i>	controlled (300)	ultrastructural changes, increased membrane permeability	TARHANEN et al. (1997)
<i>Bryoria fuscescens</i>	controlled (150)	none	RUOSS and VONARBURG (1995)
	controlled (300)	increased membrane permeability	TARHANEN et al. (1997)
<i>Collema nigrescens</i>	field fumigation (90)	decreased chlorophyll fluorescence	SCHEIDEGGER and SCHROETER (1995)
<i>Evernia prunastri</i>	field fumigation (90)	decreased chlorophyll fluorescence	SCHEIDEGGER and SCHROETER (1995)
	controlled (300)	none	CALATAYUD et al. (2000)
	controlled (150)	discolored parts	RUOSS and VONARBURG (1995)
<i>Flavoparmelia caperata</i>	OTC	none	BERTUZZI et al. (2013)
<i>Flavopunctelia flaventior</i>	controlled (80)	red photosynthesis	RIDDELL et al. (2012)
<i>Hypogymnia bitteri</i>	field fumigation (90)	decreased chlorophyll fluorescence	SCHEIDEGGER and SCHROETER (1995)
<i>Hypogymnia imshaugii</i>	controlled (80)	none	RIDDELL et al. (2012)
<i>Hypogymnia physodes</i>	controlled (300)	ultrastructural changes	TARHANEN et al. (1997)
	controlled (150)	discoloured parts	RUOSS and VONARBURG (1995)
	controlled (300)	none	CALATAYUD et al. (2000)
<i>Lobaria pulmonaria</i>	controlled (60-175)	no effect on photosynthesis	SIGAL and JOHNSTON (1986)
	field fumigation (90)	visible symptoms, decreased chlorophyll fluorescence	SCHEIDEGGER & SCHROETER (1995)
<i>Parmelia glabra</i>	controlled (150)	marginal blackening	RUOSS and VONARBURG (1995)
<i>Parmelia quercina</i>	controlled (300)	none	CALATAYUD et al. (2000)
<i>Parmelia sulcata</i>	controlled (150)	no morphological changes, discoloured parts, blackening	RUOSS and VONARBURG (1995)
	controlled (300)	none	CALATAYUD et al. (2000)
<i>Parmelia tialicea</i>	controlled (150)	discoloured parts	RUOSS and VONARBURG (1995)
<i>Parmotrema perlatum</i>	OTC	none	BERTUZZI et al. (2013)
<i>Physconia enteroxantha</i> + <i>Physconia isidiigera</i>	controlled (80)	none	RIDDELL et al. (2012)
<i>Physconia perisidiosa</i>	controlled (150)	none	RUOSS and VONARBURG (1995)
<i>Platismatia glauca</i>	controlled (150)	discoloured parts	RUOSS and VONARBURG (1995)
<i>Pseudevernia furfuracea</i>	controlled (150)	marginal blackening	RUOSS and VONARBURG (1995)
	field fumigation (90)	collapsed photobiont cells	SCHEIDEGGER and SCHROETER (1995)
<i>Pseudocyphellaria anthraspis</i>	controlled (80)	none	RIDDELL et al. (2012)
<i>Pseudoparmelia caperata</i>	controlled (100)	decreased photosynthesis	ROSS and NASH III (1983)
<i>Pseudovernia furfuracea</i>	controlled (150)	discoloured parts	RUOSS and VONARBURG (1995)
<i>Ramalina farinaceae</i>	controlled (150)	marginal blackening, discoloured parts	RUOSS and VONARBURG (1995)
<i>Ramalina fraxinea</i>	controlled (150)	marginal blackening, discoloured parts	RUOSS and VONARBURG (1995)
<i>Ramalina menziesii</i>	controlled (100)	no reduction in photosynthesis	ROSS and NASH III (1983)
	controlled (80)	none	RIDDELL et al. (2012)
<i>Usnea hirta</i>	controlled (80)	none	RIDDELL et al. (2012)
	controlled (300)	ultrastructural changes	TARHANEN et al. (1997)
<i>Usnea lapponica</i>	controlled (150)	none	RUOSS and VONARBURG (1995)
<i>Usnea rigida</i>	field fumigation (90)	visible symptoms, decreased photosynthesis	SCHEIDEGGER and SCHROETER (1995)
<i>Xanthoria parietina</i>	OTC	none	BERTUZZI et al. (2013)

BERTUZZI, S., DAVIES, L., POWER, S.A., TRETIACH, M., 2013: Ecol. Indic. 34, 391-397; CALATAYUD, A., TEMPLE, P.J., BARRENO, E., 2000: Photosynthetica 38, 281-286; RIDDELL, J., PADGETT, P.E., NASH, T.H., 2012: Environ. Pollut. 170, 202-210; ROSS, L.J., NASH, III T.H., 1983: Environ. Exp. Bot. 23, 71-77; RUOSS, E., VONARBURG, C., 1995: Cryptogam. Bot. 5, 252-263; SCHEIDEGGER, C., SCHROETER, B., 1995: Environ. Pollut. 88, 345-354; SIGAL, L.L., JOHNSTON, J.W., JR., 1986: ENVIRON. EXP. BOT. 26, 59-64; TARHANEN, S., HOLOPAINEN, T., OKSANEN, J., 1997: Ann. Bot.-London 80, 611-621.

Tab. 12: Effects of ozone exposure on vertebrates. Detailed list of all experimental studies.

<i>species</i>	<i>exposure</i>	<i>effect</i>	<i>reference</i>
<i>Bufo marinus</i>	acute	no effect on the preferred body temperatures, higher evaporative water loss rates	DOHM et al. (2001)
	acute	no effect on metabolism associated with food processing	JOHNSON et al. (2009)
	acute	depressed feeding behaviour	DOHM et al. (2008)
	acute	no differences in macrophage functions	DOHM et al. (2005)
	acute	adverse effect on immune function	DOHM and MAUTZ (2001)
<i>Cavia porcellus</i>	acute	induction of heat shock proteins	SU and GORDON (1997)
<i>Pseudacris cadaverina</i>	acute	alteration of respiration	MAUTZ and DOHM (2004)
<i>Sceloporus occidentalis</i>	acute	hypothermia	MAUTZ and DOHM (2004)

DOHM, M.R., MAUTZ, W.J., 2001: Am. Zool. 41, 1429-1429; DOHM, M.R., MAUTZ, W.J., ANDRADE, J.A., et al., 2005: Environ. Toxicol. Chem. 24, 205-210; DOHM, M.R., MAUTZ, W.J., DORATT, R.E., STEVENS, J.R., 2008: Environ. Toxicol. Chem. 27, 1209-1216; DOHM, M.R., MAUTZ, W.J., LOOBY, P.G., GELLERT, K.S., ANDRADE, J.A., 2001: Environ. Res. 86, 274-286; JOHNSON, S.R., MAUTZ, W.J., DOHM, M.R., 2009: Integr. Compar. Biol. 49, E250-E250; MAUTZ, W.J., DOHM, M.R., 2004: Comp. Biochem. Phys. A 139, 371-377; SU, W.Y., GORDON, T., 1997: J. Appl. Physiol. 83, 707-711.

Tab. 13: Number of native species for which ozone-specific foliar symptoms or ozone-like injuries have been observed in field monitoring surveys across different continents. The data are split into different descriptive groups and sites of observation.

	<i>continent of observation</i>				<i>total</i>
	<i>Europe</i>	<i>North-America</i>	<i>Central America</i>	<i>Asia</i>	
<i>total species</i>	157	49	6	33	245
<i>genera without species identification</i>	19	6	3	0	28
<i>herbaceous species</i>	69	24	1	3	97
<i>annual/biennial</i>	5	8	0	3	16
<i>perennial</i>	64	16	1	0	81
<i>woody species</i>	88	25	5	30	148
<i>deciduous</i>	77	18	1	28	124
<i>evergreen</i>	11	7	4	2	24

Service', the 'CONECOFOR (CONtrolli ECOSistemi FORestali)' program in Italy and the 'International Long-Term Ecological Studies in the Carpathian Mountains' in Europe.

Overall, the parameter "visible leaf injury" is of particular relevance for a first assessment of the relative ozone sensitivity of a species under field conditions as it indicates an overall impairment of the respective organism. Experimental verification of these ozone symptoms observed in the field (BUSSOTTI et al., 2003; GRAVANO et al., 2004; KLINE et al., 2008; SKELLY et al., 1999; VOLLENWEIDER et al., 2003) and pictorial guides of ozone effects (FLAGLER, 1998; INNES et al., 2001) helped to confirm these assessments.

In total, 49 out of 349 relevant publications provide information on the expression of foliar symptoms in the field that were attributed to ambient ozone levels. Overall, there were 528 indications for 245 native woody and herbaceous plant species and additionally for 28 genera without a species identification for which ozone-specific or ozone-like foliar symptoms have been observed in the field. Tab. 13 provides a summary of the whole data set. For herbaceous species the information is dominated by perennials, for trees and shrubs by deciduous species.

For the majority of species (60%) visible foliar symptoms due to ozone were documented in one single study only, while for 55 species symptoms were reported by at least three studies. The species with the highest number of symptom records were *Prunus serotina* (10x),

Corylus avellana (9x), *Fraxinus excelsior* (9x), *Ailanthus sylvatica* (8x), and *Fagus sylvatica* (8x), which may point to a particular ozone sensitivity of these species.

However, only ca. 30% of the species (23 herbaceous and 48 woody species) described to be responsive to ozone in these field observation studies are also subjected to controlled exposure studies shown in chapters 6.1 and 6.2, i. e. for only 71 species out of 245 the ozone response was actually verified by experimental studies. However, it points to the necessity to use both types of information for a detailed ozone cause-effect analysis for vegetation. Nevertheless, an assessment of such species-specific responses and their temporal and spatial variation based on long-term observations may be regarded as a first valuable information on a risk for biodiversity.

8 Evidence for natural selection for ozone tolerance in (semi) natural the vegetation

8.1 Spatial and temporal variations in ozone sensitivity/tolerance

The inheritance of ozone tolerance as known from crops (BURKEY and CARTER, 2009; HEGGESTAD, 1991; MEBRAHTU et al., 1990) has also been documented for wild plant species (LEE et al., 2002; WHITFIELD et al., 1997). Intraspecific variation in ozone tolerance have been evidenced for woody and herbaceous wild plant species and demonstrated that wild genotypes may differ greatly in sensi-

Tab. 14: Plant species for which spatial variation in the ozone sensitivity/tolerance was indicated by differential responses of populations from different sites; no. = number of populations or sites considered; exposure conditions for controlled sensitivity tests include exposure facility (AA, AA+ ambient air, ambient air plus ozone addition; GH greenhouse; GC growth chamber; NF non-filtered; OTC open-top chamber), ozone concentration (ppb) and duration; stat. sign. = statistically significant.

species	study area	no.	exposure conditions	stat. sign.	reference
<i>Plantago major</i>	UK	28	GC 70 ppb, 2wk	YES	REILING and DAVISON (1992)
<i>Plantago major</i>	different countries in Europe	20	GC 70 ppb, 2wk	YES	LYONS et al. (1997)
<i>Trifolium campestre</i>	Switzerland, north / south	2	OTC AA, AA+	YES	FUHRER et al. (1998)
<i>Populus tremuloides</i>	USA, eastern National Parks	5	GH 180 ppb, 6h	YES	BERRANG et al. (1986)
	USA, National Parks	15	GH 150 ppb, 6h	YES	BERRANG et al. (1991)
	USA, New York, Michigan	5	AA	YES	BERRANG et al. (1989)
	USA, Great Lakes region	6	AA	YES	KARNOSKY et al. (2003)
<i>Trifolium repens</i> <i>Trifolium pratense</i>	Switzerland	-	100 ppb, 6 d 150 ppb, 3 d	NO	NEBEL and FUHRER (1994)
<i>Phleum pratense</i>	Scandinavia	9	OTC CF+70 ppb, NF+50 ppb	NO	DANIELSSON et al. (1999)
<i>Epilobium hirsutum</i>	UK	18		NO	DAVISON and HALEY (2001)
<i>Asclepias syriaca</i>	midwestern USA	9	GH 40 to 80 ppb	NO	KLINE et al. (2009)
<i>Apocynum cannabinum</i>	midwestern USA	16	GH 40 to 80 ppb	NO	KLINE et al. (2009)
<i>Prunus serotina</i>	USA, Pennsylvania, West Virginia	15	AA	NO	LEE et al. (1999)
<i>Betula pubescens</i>	Scandinavia	5	GH 20 to 116 ppb	NO	MORTENSEN (1998)

BERRANG, P., KARNOSKY, D.F., BENNETT, J.P., 1989: Can. J. For. Res. 19, 519-522; BERRANG, P., KARNOSKY, D.F., BENNETT, J.P., 1991: Can. J. For. Res. 21, 1091-1097; BERRANG, P., KARNOSKY, D.F., MICKLER, R.A., BENNETT, J.P., 1986: Can. J. For. Res. 16, 1214-1216; DANIELSSON, H., GELANG, J., PLEIJEL, H., 1999: Environ. Exp. Bot. 42, 41-49; DAVISON, A.W., HALEY, H., 2001: In: D. Fowler, M. Coyle, R. Storeton-West, H. Lewis, T. Mansfield, N. Paul, P.S. De Silva, M. Ashmore, K. Batty, A. Davison, H. Haley (eds.), The Ozone Umbrella Project CEH Project: C00970 - Final Report, Centre for Ecology and Hydrology, Edinburgh; FUHRER, J., ENDTNER, V., BUNGENER, P., NUSSBAUM, S., GRUB, A., 1998: In: B. Boller, F.J. Stadelmann (eds.), Breeding for a multifunctional agriculture. Proceedings of the 21st Meeting of the Fodder Crops and Amenity Grasses Section of EUCARPIA, Kartause Ittingen, Switzerland, 9-12 September 1997, 191-194; KARNOSKY, D.F., PERCY, K.E., MANKOVSKA, B., PRICHARD, T., NOORMETS, A., DICKSON, R.E., JEPSEN, E., ISEBRANDS, J.G., 2003: In: D.F. Karnosky, K.E. Percy, A.H. Chappelka, C. Simpson, J. Pikkarainen (eds.), Air Pollution, Global Change and Forests in the New Millennium. Elsevier, 199-209; KLINE, L.J., DAVIS, D.D., SKELLY, J.M., DECOTEAU, D.R., 2009: North East. Nat. 16, 307-313; LEE, J.C., SKELLY, J.M., STEINER, K.C., ZHANG, J.W., SAVAGE, J.E., 1999: Environ. Pollut. 105, 325-331; LYONS, T.M., BARNES, J.D., DAVISON, A.W., 1997: New Phytol. 136, 503-510; MORTENSEN, L.M., 1998: Scand. J. Forest Res. 13, 189-196; NEBEL, B., FUHRER, J., 1994: Angew. Bot. 68, 116-121; REILING, K., DAVISON, A.W., 1992: New Phytol. 122, 699-708.

vity. Species for which this has been shown are *Populus tremuloides* (KARNOSKY et al., 1992; KARNOSKY et al., 2003A); *P. tremuloides* × *P. tremula* L. (OKSANEN et al., 2001); *Prunus serotina* (LEE et al., 1999); *Betula pendula* (OKSANEN, 2003; PÄÄKKÖNEN et al., 1993; PÄÄKKÖNEN et al., 1996); *Pinus densiflora* (LEE et al., 2006); *Pinus taeda* (TAYLOR, 1994); *Quercus coccifera* (ELVIRA et al., 2003); *Anthoxanthum odoratum* (DAWNAY and MILLS, 2009); *Arabidopsis thaliana* (BROSCHÉ et al., 2010); *Phleum pratense* and *Phleum alpinum* (DANIELSSON et al., 1999).

With respect of steadily increasing ozone exposure levels over the last decades it has been hypothesised that this could also have resulted in an increase of the ozone tolerance of native (plant) species. There are several studies reporting on spatial approaches to test whether geographically separated plant populations, which were exposed to different levels of ozone over many years exhibit differences in their ozone sensitivity/tolerance corresponding to the prevailing ozone exposure regime at the respective site. The degree of the sensitivity/tolerance of a population was tested experimentally under controlled exposure conditions. In Tab. 14 we have compiled studies where associations between the ozone sensitivity/tolerance of a plant population and the “ozone climate” at different location have been demonstrated.

The most prominent example of spatial variation in ozone tolerance is the herbaceous wild plant species *Plantago major* (Tab. 14). Testing the relative ozone sensitivity/tolerance of 28 geographically separated populations, which had been collected across UK, it was

demonstrated that the populations differed in their ozone sensitivity/tolerance and that these differences were statistically related primarily to the “ozone climate” of its site of origin (LYONS et al., 1997; PEARSON et al., 1996; REILING and DAVISON, 1992). However, as also shown in Tab. 14, in some studies intraspecific differences in ozone sensitivity/tolerance between populations originating from different proveniences were also shown, but a correlation with the “ozone climate” could not statistically be verified (Tab. 14). This was partly explained by a high variability in the ozone sensitivity/tolerance of the individuals within the populations (KLINE et al., 2009).

In addition to spatial variations for *Plantago major* also a temporal change in ozone resistance/tolerance over a short period of time was reported. For two populations in UK an increase in ozone tolerance has been shown in experiments for plants grown from seed material collected after summers when ozone concentrations were high (DAVISON and REILING, 1995; WHITFIELD et al., 1997). HEAGLE et al. (1991) exposed *Trifolium repens* plants under field conditions to different levels of ozone under conditions of intra- and interspecific competition with *Festuca arundinacea* and propagated those individuals by cloning that survived the ozone treatment. Only after two years clones sampled from the high ozone plots exhibited a higher percentage of ozone tolerant clones than those treated with low ozone. In contrast, repeated exposure of *Betula pendula* trees to ozone for six years led to an increase in the ozone sensitivity of the trees, which was partly explained by an ozone induced change in the growth form and deleterious carry-over effects (OKSANEN, 2003).

8.2 Implication of variation in ozone tolerance for the genetic structure of plant populations

Any indication of a loss of ozone sensitive genotypes in areas with high ozone pollution carries the risk for a loss of useful rare alleles, particularly, if some genes are found exclusively in the sensitive genotypes as this has been suggested by isozyme studies of *Picea abies* clones (KARNOSKY et al., 1989A). As a consequence, ozone pollution would have the potential to affect the genetic structure of plant populations. For example, the finding that ozone and/or pollutant sensitive genotypes are under-represented within populations of plant species in eastern North America was interpreted as a first stage of natural selection, i.e. the elimination of sensitive genotypes attributed to the impact of ozone and/or other regional air pollutants (BERRANG et al., 1991; KARNOSKY et al., 1989A; B).

There is evidence that micro-evolutionary processes could take place in response to long-term elevated ozone exposure and at some regions even the prevailing ambient ozone levels are sufficiently high to promote this evolution (BERRANG et al., 1991; 1986; KOLLIKER et al., 2008; LYONS et al., 1997). There are some indications for this assumption in the literature for both trees and herbaceous plants. STASZAK et al. (2004) reported on a relationship between ozone injury of *Pinus ponderosa* needles and heterozygosity, as ozone tolerant trees were more heterozygous than ozone sensitive individuals. Moreover, the signatures of the genetic structure between saplings and mature pine trees suggest that the increase in air pollution over the last 50 years together with episodic drought stress may have affected the genetic structure of two pine species in the US Sequoia National Park (STASZAK et al., 2007). WOLFF et al. (2000) analysed genetic markers associated with ozone tolerance in *Plantago major* at 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 a selection of 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 the authors concluded that plants with similar degrees of ozone tolerance are not closely related (DAVISON and REILING, 1995; WHITFIELD et al., 1997). KOLLIKER et al. (2008) recently demonstrated that differences in the genetic composition and diversity were only detectable in populations of the species *Plantago lanceolata* after exposure of an old semi-natural grassland to elevated ozone for five years.

BASSIN et al. (2004) examined the genetic distinctiveness of five *Centaurea jacea* populations originating from different European countries (Norway, Hungary, Switzerland, Italy, Slovenia) showing a high degree of intraspecific 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 (DAVISON et al., 2003). According to KARNOSKY et al. (1989A) 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.

Conclusion

There is currently insufficient information available, if and to what extent tropospheric ozone might contribute to biodiversity changes in terrestrial ecosystems. As a first step into such an assessment the relative ozone sensitivity of the respective organisms should be known. Therefore, the aim of the present study was to systematically analyse possible ozone impacts on different taxa and species through a literature research. Worldwide information was collected about 350 varieties across 54 crop plant species and 465 vascular and fern

plant species belonging to (semi)-natural vegetation types and used as a database. Overall, the available ozone studies covered only a small fraction of the entire global flora, e.g. for Germany only about 6.1% of all known plant species.

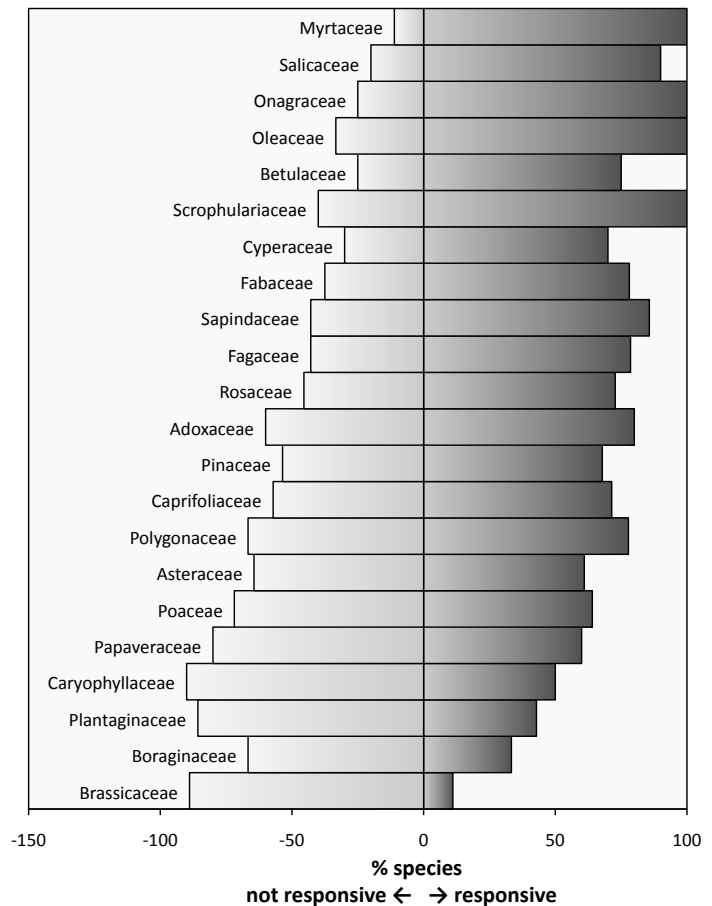


Fig. 1: Ranking of ozone sensitivity of native herbaceous or woody plant species based on their taxonomic classification. Percentage of the number of ozone responsive and non-responsive species within a family are shown (according to Chap. 6, Tab. 3 and Tab. 7). Only those families are considered which are represented by at least five different species.

About two third of woody and about one half of herbaceous vascular species listed in the database were described as ozone sensitive in at least one study. These proportions are slightly higher for visible leaf injury than for growth effects and herbaceous and deciduous woody plants are more responsive to ozone than grasses and coniferous trees.

Based on this information we make an attempt to identify and rank plant families according to the proportion of ozone sensitive species within a particular family as shown in Fig. 1. For example, while many species in the family of Myrtaceae and Salicaceae seem to be rather sensitive towards ozone this is not true for the Boraginaceae and the Brassicaceae.

With respect to the German situation there is evidence from the database that a number of plant species that are already categorised as endangered or near-threatened (Tab. 4) seem to be sensitive towards an ozone exposure. Probably, these plant species should be more thoroughly observed under aspects of air pollution impacts.

In addition the present database has shown that there is some evidence that ozone pollution in the past has affected plant selection and modified the genetic pool of genotypes. Although there is still

unsufficient evidence whether rapid changes in plant tolerance to ozone impacts is an overall phenomenon in non-managed ecosystems. However, due to a broad intraspecific variation of ozone sensitivity of plant species it has to be kept in mind that classifying a species as either ozone sensitive or tolerant might be an oversimplification because the ozone response of a particular genotype seems to reflect its ozone exposure history rather than a generic species specific trait. In the context of ozone risk assessments for biodiversity this must be taken into account.

Information on direct effects of ozone on species other than vascular plants (mosses, ferns, lichens, algae, fungi, vertebrates) is very poor and does not allow a sensitivity assessment. Other organisms like microorganisms, arthropods or insects are known to not respond directly to ambient ozone, but to be affected indirectly via impairment of the vitality of plants they are associated with (WEIGEL et al., 2015). These organisms were not considered here. Also, we did not consider if and to what extent other environmental factors (e.g. drought, nutrient limitation, climate change, elevated CO₂) modify the response of a particular species or genotype to ozone. Nevertheless, the information summarised provided in the present study provides sufficient evidence that current tropospheric ozone levels interact with many elements of the terrestrial biodiversity.

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