Plant-Mediated Ecosystem Effects of Tropospheric Ozone

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Abstract Tropospheric ozone (O_3) is considered as the most significant phytotoxic pollutant in the atmosphere and is already responsible for widespread effects on crops, trees and native plant species. Globally, there is evidence that the background O_3 concentrations are further increasing. Most research has been conducted on plant and tree species of commercial value, but very little is known about the impacts of O_3 on the scale of forest-, agro- or grassland ecosystems. Exposure to elevated O_3 causes oxidative stress, which results in reduced photosynthesis, visible injury, decreased growth and productivity. We present examples showing that impacts of O_3 on vegetation may lead to long-term effects on ecosystem structure and function. Recent experiments have shown that O_3 can cause a shift in plant

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species composition and can indirectly affect soil processes. Ozone has also been shown to affect water cycling through its effect on stomata and can alter overall ecosystem productivity.

1 Introduction

During the last 60 years tropospheric or ground-level ozone (O_3) has emerged as an air pollution problem of global dimension with respect to its harmful impacts on human health and vegetation (Akimoto 2003; Royal Society 2008). As a secondary air pollutant O_3 is formed in the troposphere through a number of sunlight driven photochemical reactions involving the main precursor substances: nitrogen mono- and dioxide (NO/NO_2), volatile organic compounds (VOC), methane (CH_4) and carbon monoxide (CO) (Staehelin 2001). These precursors are produced naturally or emitted from anthropogenic activities such as vehicles, power plants, biomass burning and all other forms of combustion.

Terrestrial ecosystems are the major sink for tropospheric O_3 and consequently, vegetation is at particular risk from this pollutant. Ozone enters the plant interior through the stomata and as a strong oxidant O_3 and its breakdown products, respectively, are able to impact plants by altering plant cellular functions and by reducing photosynthesis and changing other important physiological functions. Collectively, this may result in visible leaf injury, growth and biomass reduction and overall inferior plant vigour (Ashmore 2005; Booker et al. 2009; Matyssek et al. 2010a, b). Whether or not these effects at the single plant level have implications or are relevant in an ecosystem context is still a matter of debate (Laurence and Andersen 2003).

In the past four decades O_3 effects have been thoroughly investigated with crops (reviewed by, e.g. Heagle 1989; Fiscus et al. 2005; Booker et al. 2009; Mills and Harmens 2011) and particularly with deciduous and coniferous trees (reviewed e.g. by; Sandermann et al. 1997; Percy et al. 2003a, b; Matyssek et al. 2010a, b, 2013). Other types of natural or semi-natural vegetation have only recently and to a lesser extent received attention (reviewed by, e.g. Fuhrer 1997; Davison and Barnes 1998; Ashmore 2005; Hayes et al. 2007). While the interest related to O_3 effects on crops and commercially relevant trees was mainly driven by concerns about the potential economic losses, the more recent emphasis in assessing its potential effects on ecosystem integrity and related ecosystem functions and services is based on concerns of the potential threats of O_3 to the biodiversity of these habitats, and the long-term, more subtle impacts on ecosystem functions and services such as carbon sequestration, nutrient cycling, water relations and pollination.

While there is a wealth of information on O_3 effects on plant metabolism and plant growth, respectively (e.g. Fiscus et al. 2005; Heath 2008; Booker et al. 2009; Cho et al. 2011), it is the intention of the present contribution to report on the progress that emerged from O_3 effects research with different types of vegetation during the last approx. 15 years with an emphasis on studies that addressed potential implications of this pollutant in an ecosystem context. With this objective we will not address and discuss the large body of information that has emerged during this period with respect to adequate O_3 risk assessments for vegetation, particularly with regard to the progress that has been made in describing phytotoxically relevant "absorbed O_3 doses" by overcoming the concept of O_3 exposure of vegetation (e.g. Matyssek et al. 2013). Rather, we focus on a more qualitative description of potential O_3 effects on plants and ecosystems, respectively, primarily without considering dose–response relationships.

In the following sections we first describe current and future O_3 exposure scenarios and the most common methods by which O_3 effects on vegetation are assessed. We then briefly summarise the current understanding of O_3-induced impairments at the individual plant level that are relevant for the understanding of its ecosystem effects (Fig. 1). Predominately we then address selected examples of how these O_3 effects relate to the ecosystem level, and consider and discuss results that are equally relevant for managed and unmanaged, natural ecosystems.

2 Ozone Levels: Trends and Variation in Space and Time

Naturally occurring O_3 concentrations in the troposphere (ground-level) in the pre-industrial era have been described to range between approx. 5–20 parts per billion (ppb) (Marenco et al. 1994). Since the pre-industrial era the global annual mean background O_3 concentrations have increased considerably to values between approx. $>$20–45 ppb depending on the geographical location (Vingarzan 2004) with a rate of increase in the annual mean values ranging between 0.1 and 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 industrialisation and hence increasing emissions of precursors of O_3. In these countries, O_3 has reached levels in ambient air which are of concern with respect to vegetation damage and human health effects (Emberson et al. 2003; Royal Society 2008).

The pattern of O_3 exposure of vegetation is changing on a global scale. While in large parts of Western Europe, North America and Japan, a trend of decreasing frequencies of O_3 peak values ("photosmog episodes") can be observed due to control measures on the emission of the precursor compounds, background O_3 values are increasing (Oltmans et al. 2006; Jonson et al. 2006). In the northern hemisphere at mid-latitudes, mean values at background sites have been increasing by 0.5–2 % per year (Derwent 2008). Future changes of the O_3 levels will be determined by the trends of the emissions of the precursors and of temperature and solar radiation. Ongoing global population growth coupled to increasing demands for resources such as land, fossil fuels and polluting activities like energy production, agriculture and transport will lead to enhanced production of natural and

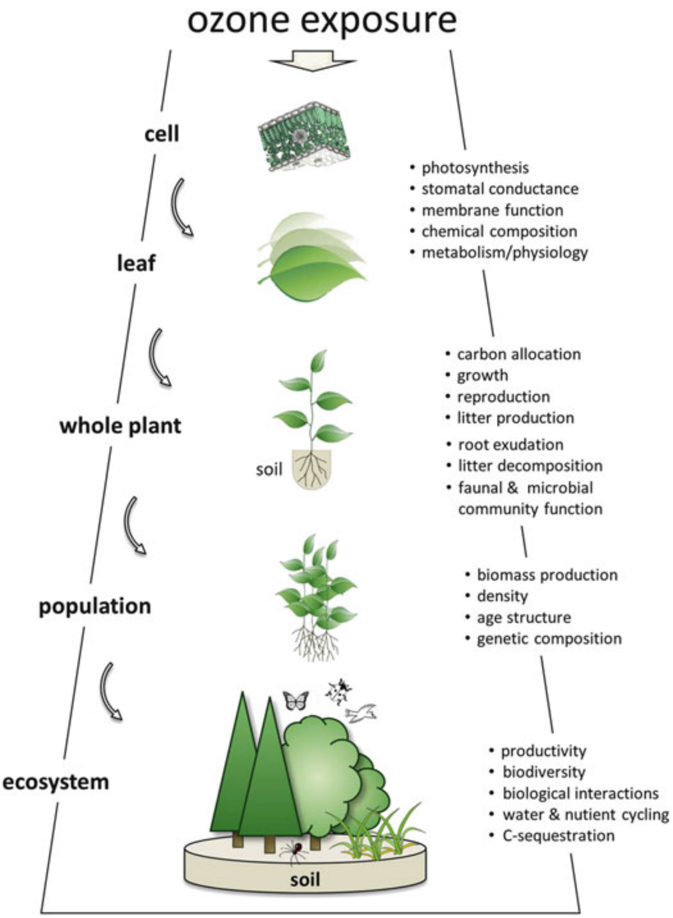

Fig. 1 General scheme of major endpoints that are affected by O_3 exposure at different levels of biological organisation in plants and ecosystems

anthropogenic O_3 precursors like VOC's, NO_x, CH_4 and CO. Higher surface temperatures along with climate change may also trigger the formation of surface O_3 levels. While predictive models, e.g. based on IPCC-SRES global emission scenarios, indicate that background O_3 concentrations will continue to increase at a rate of 0.5–2 % per year in the Northern Hemisphere during the next 100 years and will be in the range of ca. 42–84 ppb by 2100 (Prather et al. 2003; Vingarzan 2004; Jacob and Winner 2009; Fig. 2), recent models predict more moderate increases of O_3 levels until 2050 (Wild et al. 2012). These changes of the global O_3 exposure will be accompanied by other predicted changes in atmospheric chemistry (e.g. increasing atmospheric CO_2 concentrations) and climate which again may modify O_3 effects in the future.

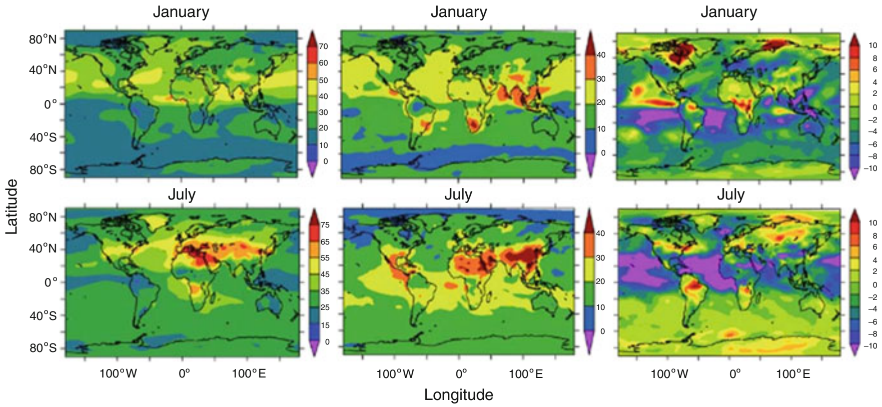

Fig. 2 Modelled surface O_3 (ppb) in January and July from the present-day simulation (*left*) and changes in surface O_3 (ppb) between 2000 and 2100 due to anthropogenic emission changes (*right*). Reprinted from Zeng et al. (2008)

Ozone concentrations influenced by human activities vary significantly with time (diurnally, seasonally, inter-annually) and with geographic location. This variability is of particular relevance for the effects on vegetation, as different vegetation types or developmental stages of plants, respectively, may be exposed to very different levels of O_3 during the course of the year. As O_3 formation is dependent on sunlight and as some of the chemical reactions involved in the O_3 formation in the troposphere are temperature-dependent, O_3 concentrations are particularly high at warm sunny days (Royal Society 2008). This link to the weather conditions also contributes to the inter-annual variation of O_3 concentrations. At least in large parts of Europe, peak O_3 concentrations occur especially in spring and summer. While at low elevation sites O_3 concentrations show diurnal cycles with low concentrations during the night and in the morning and high and peak concentration during the afternoon, high elevation sites mostly do not show such distinct diurnal variation (Stockwell et al. 1997). In general, at a particular location the build-up of phytotoxic O_3 concentrations depends on the local meteorology, the topography and the regional sources of O_3 precursors.

3 Methods to Study Ozone Impacts

The interpretation of plant responses to O_3 to a large extend depends on the methodology that is used to study its impacts. Therefore, a brief description of the most prominent methods in O_3 effects research is given here. Methods to investigate O_3 effects on vegetation can broadly be categorised into methods involving experimental exposure to O_3 and methods where plants are exposed to O_3 in ambient air. Each method has its particular advantages or disadvantages and its usefulness depends on the questions to be addressed and the objectives and budgetary circumstances of the respective study (Manning and Krupa 1992). Experimental techniques to expose single plants, plant communities and segments of ecosystems to modified O_3 concentrations range from controlled environmental chambers, greenhouses, field chambers to open-air O_3 exposure systems. Most of the information of the effects of O_3 on plants is derived from the use of various types of indoor and outdoor chambers.

Laboratory fumigation chambers of various designs (e.g. Heck et al. 1978; Payer et al. 1993) which provide highly reproducible environmental and O_3 exposure conditions have widely been used for assessing visible injury or physiological and biochemical O_3 effects. However, due to different microclimatic conditions in the chambers compared to open air ("chamber effects"), plants often show morphological or physiological differences compared to field-grown plants. Moreover, laboratory chambers are limited in space and mostly only useful for small scale pot or mesocosm studies. To overcome some of these limitations, open-top chambers (OTCs) were developed (Heagle et al. 1973) and have been the most widely used O_3 exposure system up to now (e.g. Heagle et al. 1988; Jäger et al. 1999; Zheng et al. 2013; Oksanen et al. 2013; Burkart et al. 2013). In OTCs, plants can be grown in their natural soil environment, in pots or as artificial model communities (mesocosms). Air either enriched with O_3 or filtered to remove O_3 from ambient air is introduced into the chamber with a blower system. Open-top chambers are best suited for in situ studies with low stature vegetation, e.g. like most crop or grassland species. As with the laboratory fumigation chambers for the interpretation of O_3 effects, the chamber microclimate may interfere with O_3 effects. For example, when used in species-rich systems like in certain grasslands, the differences between the ambient and OTC climate can lead to changes in vegetation structure in the chambers in comparison to chamberless ambient air plots (Grünhage and Jäger 2003).

To allow studies with taller trees, large versions of OTCs have been constructed (Musselman and Hale 1997). According to Kolb and Matyssek (2001) chamber studies with trees cover only a short period of the entire life history of a forest stand; they are thus limited in predicting longer-term ecosystem effects of O_3.

To overcome the various types of "chamber effects" in any kind of enclosure system used for O_3 effect studies and to overcome space limitations and restricted plant root volumes, respectively, chamberless O_3 exposure facilities have been developed (McLeod 1995). The most often used chamberless exposure system for O_3 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 O_3 into plant canopies. During the last two decades large-scale FACE-type O_3 exposure systems have been employed in O_3 effects studies with crops like soybean (Morgan et al. 2004), rice and wheat (Tang et al. 2011), and young tree species (Karnosky et al. 1999). A similar custom-designed circular free air O_3 exposure system was used by Volk et al. (2003) in a Swiss grassland system. A free air O_3 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. (2010a, b, 2013). A similar system has recently been established in northern Japan addressing potential impacts of O_3 on deciduous oak and white birch (Watanabe et al. 2013). FACE-type O_3 exposure systems require sophisticated infrastructures and can be only used to increase O_3 levels in ambient air. In free air O_3 exposure systems, the coupling between the atmosphere and the plant canopy as well as between the canopy and the respective soil volume largely remains unchanged. Thus, in situ water and nutrient fluxes at the ecosystem level can be investigated. Ideally, FACE type O_3 exposure systems allow O_3 effect research at various hierarchical levels, for example, to link molecular biology with ecophysiological research.

Among the methods of O_3 exposure where there is no manipulation of the O_3 concentration surrounding the plants are ambient gradient studies. Plants or plant community responses are examined along gradients of O_3 concentrations across a landscape or regional transect providing multiple levels of exposure to O_3 that are naturally occurring. Forest tree species and ecosystem responses to O_3 in the USA have been assessed using gradient studies (Winner et al. 1989; McLaughlin et al. 2007a, b). Examples of other methods to assess O_3 effects on plants are the use of protecting chemicals against O_3 stress (Manning et al. 2011), biomonitoring techniques using indicator plants (Manning et al. 2002) and the use of plant growth models (Martin et al. 2001; Hogsett et al. 2008).

4 Ozone Impacts at the Single Plant Level

Ozone impacts on ecosystems result from excessive uptake of O_3 by plants, direct toxicity and cell damage, or from indirect effects mediated by the individual organisms. Although extrapolation of results from studies with individual plants or plant assemblages to the ecosystem level is difficult to make, the knowledge of the processes and mechanisms by which plants are affected by O_3 is an essential prerequisite to understand ecosystem responses to O_3. In this section, we briefly summarise the current understanding of the major mechanisms of O_3 effects at the individual plant scale governing vegetation response to O_3 including uptake, altered physiology such as stomatal functioning, photosynthesis, carbon allocation, reduced growth (above- and below-ground) and reproduction. These individual plant-scale responses to O_3 in the short term may lead to long-term changes in species and genetic composition, changes in water economy and functioning of species communities and, hence, ecosystem structure and function (Sect. 5).

4.1 Deposition of O_3 and Plant Uptake

Vegetation is an important natural sink for O_3. Ozone is transferred from the atmosphere onto plant canopies by turbulent diffusion (deposition), which is

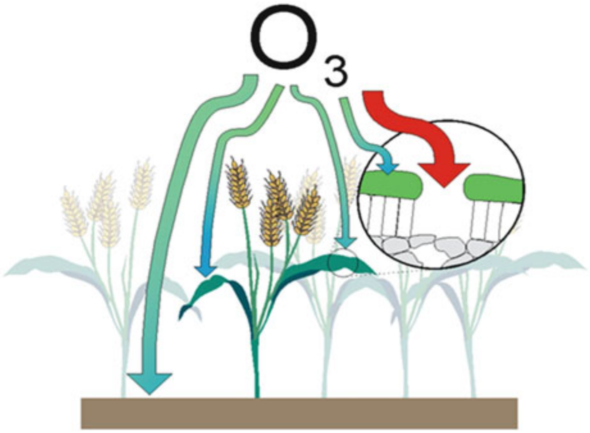

Fig. 3 Major pathways of the transfer of O_3 to terrestrial surfaces. The uptake by vegetation is attributed to both stomatal and non-stomatal (external plant surfaces and soil) deposition. The thickness of the *arrows* denotes the relative importance of the respective pathway. Reprinted with permission from Dr. Lisa Emberson, SEI York, UK

governed by micro-meteorological conditions (radiation, temperature, wind, etc.) and the roughness of the vegetation. The uptake of O_3 by vegetation is attributed to both non-stomatal and stomatal deposition (Fig. 3). Non-stomatal deposition includes deposition to soil, stems, cuticles and other external surfaces. It has long been known (Kerstiens and Lendzian 1989; Massman and Grantz 1995) that penetration of O_3 through the plant cuticle is of minor importance in comparison to the route of uptake through the stomata. This transfer of the gas through the atmosphere (turbulent diffusion) into the plant via molecular diffusion through the stomata is currently considered the key process in relating O_3 exposure to plant responses (Fowler et al. 2009; Fig. 3). Consequently, all environmental factors that modify the stomatal aperture (e.g. temperature, light and soil water conditions, other pollutants, atmospheric CO_2 concentration) and which thus affect leaf gas exchange have an influence on the uptake of O_3 into the plant interior (Fiscus et al. 2005; Fuhrer 2009).

Field measurements of O_3 deposition (flux) in various ecosystems indicate that total dry deposition is largely dominated by stomatal uptake during the most active parts of the growing season, but, at other times of the year and depending on vegetation type and weather conditions, non-stomatal deposition can be larger than stomatal uptake (Cieslik 2004; Cape et al. 2009). For example, continuous multi-year O_3 flux measurements over moorland vegetation in Scotland indicated that over a seasonal scale non-stomatal deposition dominated the overall O_3 flux and represented 70 % of the total O_3 deposition (Fowler et al. 2001). Nunn et al. (2010) compared sap flow measurements—i.e. tree level transpiration—and eddy co-variance approaches—i.e. stand level transpiration—in mixed beech/spruce stands and found that stomatal O_3 flux amounted to 33 % of the total stand O_3 flux. The concentration of O_3 diminishes as one moves down a canopy to the soil. In addition, gas-phase reactions between O_3 and biogenic volatile organic compounds (BVOCs) and nitric oxide (NO) emitted from the ecosystem contribute to the removal of O_3 from the atmosphere (Fares et al. 2010). Canopy architecture and the density of the foliage may also determine to which O_3 concentration individual leaves are finally exposed. For example, in comparison to dense plant canopies, in open canopies like in widely spaced crop rows leaves inside the canopy will be exposed to similar O_3 concentration as at the canopy surface.

4.2 Effects on Stomatal Functioning

There has been long-term and widespread evidence that elevated O_3 levels alter stomatal performance and hence stomatal conductance (g_s) of various plant species (Darrall 1989; Mansfield 1998; Robinson et al. 1998). However, the type of stomatal responses to O_3 exposure is still not fully clear. While high O_3 concentrations appear to reduce g_s, there are variable results under more moderate O_3 levels, i.e. those resembling current ambient conditions (Paoletti and Grulke 2005; Wittig et al. 2007). For example, under chronic exposure conditions O_3 may lead either to enhanced stomatal aperture and a delayed stomatal closure during the night or to a reduction of the stomatal conductance. Moreover, exposure to O_3 has been shown to aggravate the heterogeneous stomatal aperture across the leaf surface, which is known as patchiness (Beyschlag and Eckstein 1998). This increase of stomatal patchiness upon O_3 exposure implies that only the integrated response of groups of stomata will determine the response to O_3 at the larger scales of the total plant and the canopy, respectively (Paoletti and Grulke 2005).

Stomata closure and reduced g_s due to O_3 exposure are often found when measured under steady-state high light conditions. In a recent meta-analysis (Wittig et al. 2007), which compiled results of 73 primary research articles of O_3 effects on photosynthesis and g_s of various tree species, the authors found that the O_3 levels in the atmosphere today suppresses g_s by, on average, 13 % compared to pre-industrial O_3 levels. When ambient background versus elevated O_3 was compared, g_s decreased by 6 % in the elevated O_3 treatment. Evidence for an O_3-induced stomatal closure is also available from recent studies with crops under chamberless O_3 exposure (Morgan et al. 2003; Kitao et al. 2009). Current assumptions of the possible mechanisms that may explain O_3-induced stomatal closure include (1) reduced photosynthesis and increased substomatal CO_2 concentration, (2) direct impact on guard cells, (3) altered calcium homeostasis or (4) altered hormone production (McAinsh et al. 2002; Wittig et al. 2007; Wilkinson and Davies 2010). Overall, this kind of stomatal responses implies that plants are protected from water loss.

However, often the measurements of g_s were carried out under conditions that normally do not prevail in the field in the course of a day, i.e. high light and steady-state vapour pressure deficit. Consequently, when measurements are compared that were carried out under more variable environmental conditions, stomatal aperture was not uniformly decreased by O_3 during the day. Such a “sluggish” stomatal response has long been known (Keller and Häsler 1984) and describes the delay in stomatal response to changing environmental factors relative to controls (Paoletti and Grulke 2010). Sluggish stomatal responses have been observed in O_3 effect studies, e.g. with tree (Wallin and Skarby 1992; Matyssek et al. 1995; Grulke et al. 2007) or grass species (Mills et al. 2009). Thus, if stomata fail to close under low light or water-stressed conditions, water loss may be greater over time. In other situations, it is possible that sluggish stomata may fail to completely open in response to environmental stimuli and result in decreased water loss.

As O_3 may affect plant stomata in relation to the response to other environmental variables like vapour pressure deficit, drought and light (Uddling et al. 2009; McAinsh et al. 2002; Paoletti and Grulke 2010), the resulting stomatal sluggishness may result in increasing g_s and hence increased water use under conditions which normally induce stomatal closure (e.g. drought, high vapour pressure deficit and low light). Such an increase of g_s even under reduced water supply in response to O_3 exposure was observed in several recent studies with grassland species (Mills et al. 2009; Wilkinson and Davies 2010; Hayes et al. 2012). It was suggested that O_3 can prevent stomatal closure under drought by altering the sensitivity of stomata to abscisic acid, a plant hormone stimulating stomatal closure under drought conditions (Wilkinson and Davies 2010; Wilkinson et al. 2012).

There are also recent research results, where O_3 apparently has no effects on stomata at all. In a multi-year FACE-type exposure of soybean to O_3 concentrations predicted by approx. 2050, there were no significant effects on midday g_s, and no effects on instantaneous g_s on 13 of the 15 measurement days (Bernacchi et al. 2006).

Ozone-induced physiological changes, such as reduced leaf area index and accelerated leaf senescence, have also been suggested to have an effect on water-use efficiency of plants. For example, some previous and more recent chamber and field studies have shown that that O_3 exposure is correlated with lower foliar retention (e.g. Karnosky et al. 1996, 2003; Topa et al. 2001).

Overall, there is still a high variability in the results of stomata responses to an O_3 exposure (Table 1). Thus, a better understanding of O_3 effects on leaf stomatal

Table 1 Summary of studies investigating O_3 effects on stomatal functioning in trees, crops and grassland species [after Mills et al. (2013)]

	Total number	No effect	Sluggish control	Increased opening	Stomatal closing
Crops (no. of species)	16	1	2	1	12
Crops (no. of experiments)	22	2	2	1	17
Trees (no. of species)	44	12	4	13	15
Trees (no. of experiments)	60	12	10	17	21
Grasslands (no. of species)	8	2	1	2	3
Grasslands (no. of expts.)	11	2	1	5	3
Total (no. of species)	68	15	7	16	30
Total (no. of experiments)	93	16	13	23	41
Ozone range (ppb) (25th to 75th percentile)		35–80	70–120	50–90	59–100
Mean ozone concentration		59 ppb	91 ppb	67 ppb	89 ppb

functioning remains a challenge, as this type of O_3 impacts on plants may have wider implications for the overall hydrology at the ecosystem level (see Sect. 5.1).

4.3 Physiological Effects

Once O_3 molecules have passed the stomatal pore, its subsequent effects on the plant include reactions with the apoplastic fluid and generation of reactive oxygen species (ROS), effects on the cell membrane structure and function, changes of cell metabolism and cellular events, which finally result in the generation of observable plant responses like chlorotic or necrotic tissue damage, reduced photosynthesis, temporal shifts in the plant's development and losses in productivity (Cho et al. 2011; Dizengremel et al. 2013; Fig. 1).

In the substomatal cavity O_3 rapidly reacts with water which results in the generation of ROS like hydrogen peroxide, singlet oxygen and hydroxyl radicals and with various compounds in the adjacent cell walls or on their outer cell membranes (Iriti and Faoro 2008). Based on this rapid chemical turnover, it has long been assumed that the O_3 concentration in the substomatal cavity is close to zero (Laisk et al. 1989); however, there is no unequivocal evidence for this assumption. According to the present understanding the reaction products of O_3 with the apoplastic fluid and with various biomolecules, respectively, are assumed to interfere with a signalling pathway of the plant cell which is related to cell death and which is triggered by ROS (e.g. Baier et al. 2005; Kangasjarvi et al. 2005; Cho et al. 2011). Apoplastic antioxidants (e.g. ascorbic acid, glutathione), the role of which is to protect cell membranes from a ROS attack, can interfere with O_3 or its reaction products. For example, reaction with the apoplastic acorbate pool seems to be a particular important process for ROS detoxification and is believed to be the first line of defence against O_3 injury, although other defence compounds may also be involved (Fiscus et al. 2005; Fuhrer 2009). Detoxification occurs from both existing antioxidants and those stimulated by O_3 itself. Defence reactions require energy for regeneration of antioxidants, i.e. particularly at prolonged O_3 exposure detoxification capacity may decline due to decreased rates of carbon assimilation and limited available energy (Wieser and Matyssek 2007). In general, cell injury or death of plant tissues occurs when the O_3 uptake exceeds the detoxification capacity. ROS that remain unscavenged can cause a variety of leaf injury symptoms such as necrotic stippling, bronzing, chlorosis or premature senescence.

Visible injury resulting from ambient O_3 pollution has been observed on a wide range of plant species including trees, crops and species of semi-natural vegetation in North-America and in Europe (Flagler 1998; Innes et al. 2001; Mills et al. 2010) and is usually classified as acute or chronic. While acute injury involves the death of the cells and develops within a few hours or days following exposure to high pollutant levels, chronic injury typically develops more slowly within days or weeks following O_3 exposure. While on broad-leaved plants visible injuries include stippling, flecking, surface bleaching, bifacial necrosis, pigmentation (e.g. bronzing) and chlorosis, for conifers visible injury includes chlorotic banding, tip-burn, flecking and chlorotic mottling (Flagler 1998). For both plant types O_3-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. The extent of O_3-induced visible foliar injury is often related to the amount of soil moisture available to the respective plants during the year in which the visible foliar injury is being assessed. As drought conditions generally decreases stomatal conductance and limit the amount of O_3 entering the plant leaf, the result can be less injury. Several studies have shown that dry periods in local areas tend to decrease the incidence and severity of O_3-induced visible foliar injury (Matyssek et al. 2006; Grulke et al. 2003). Therefore, the incidence of visible foliar injury is not always higher in years and areas with higher O_3.

Ozone-induced visible injury is of particular significance when the quality and the marketable value of a plant depend on the appearance of the foliage. Such O_3 damage has been observed on a number of horticultural crops in several countries (Fumagalli et al. 2001; Kostka-Rick et al. 2002; Sheu and Liu 2003).

At chronic O_3 exposure, visible injury is often not observed, but decreased rates of CO_2 assimilation indicate adverse O_3 effects on plant vitality. The response of photosynthesis to O_3 has received much attention in order to explain O_3-induced losses of plant productivity in a wide variety of tree and crop species as well as in grassland and other native plant species (Reich 1987; Morgan et al. 2003; Fiscus et al. 2005; Wittig et al. 2007; Booker et al. 2009; Fuhrer 2009). It may be assumed that plant growth retardation under longer-term O_3 exposure at moderately enhanced concentrations is mostly the result of reduced rates of assimilation at the leaf level, although within-tree alterations of carbon allocation due to disturbed phytohormonal regulation have also been shown to affect tree growth (Winwood et al. 2007; Kitao et al. 2012). For example, a recent analysis of results from different experimental O_3 fumigation studies with tree species covering ambient or near-ambient O_3 concentrations revealed that O_3 levels of approximately 40 ppb can suppress net assimilation rate on average by 11 % compared with pre-industrial (10 ppb) O_3 exposure conditions (Wittig et al. 2007). Summarising 53 O_3 exposure studies with soybean in a meta-analytic approach Morgan et al. (2003) found a ca. 20 % reduction in net assimilation rate due to an average O_3 exposure of 70 ppb.

The impairment of photosynthesis by O_3 has been attributed to effects on the electron transport system (light reactions), a decline in the efficiency of carboxylation (dark reactions), and indirect effects on stomata, i.e. lower rates of diffusion of CO_2 into the leaf interior (Paoletti and Grulke 2005).

Recent studies with plants of natural ecosystems (Scebba et al. 2006), tree species (maple: Calatayud et al. 2007) and crops (tomato: Degl'Innocenti et al. 2007; soybean: Singh et al. 2009), particularly using chlorophyll fluorescence as a measurement tool, have shown that O_3 can alter photosynthetic processes at the level of the electron transport. The effects were connected with decreases in leaf chlorophyll content, reduction in the efficiency of excitation capture, reduced numbers of intact or open photosystem II reaction centres or increases in dissipation of energy through heat.

However, loss of carbon assimilation capacity is mostly considered as the primary reason for a decline of photosynthesis under O_3 exposure. This reduction in carbon assimilation is primarily the result of an O_3-induced decline in the amount and activity of Rubisco (Long and Naidu 2002; Matyssek and Sandermann 2003; Singh et al. 2009). Both, a decrease in Rubisco synthesis and an enhanced degradation of the protein contribute to the measured reduction in its quantity. This impairment of Rubisco is accompanied by a loss of the mRNA coding for the small (rbcS) and large (rbcL) subunits of the enzyme. For example, declines in rbcS mRNA were measured in beech saplings in a free air O_3 exposure system (Olbrich et al. 2009). Effects of O_3 on proteins involved in carbon assimilation have also been observed, as reductions in quantities of the small and large subunit (rbcL) of Rubisco and Rubisco activase were measured in soybean plants exposed to 120 ppb O_3 for 3 days (Ahsan et al. 2010). Similar results were observed with wheat (approx. 70 ppb O_3 for 50 days for 5 h day^{-1}) (Sarkar and Agrawal 2010).

Overall recent research results confirm earlier studies that decreased photosynthesis is commonly observed in plants grown under elevated O_3 concentration. Although many different changes are observed in the photosynthetic apparatus, decreased activity and amount of Rubisco appear to be the prevailing causes of loss of photosynthetic capacity.

4.4 Effects on Growth and Reproduction

Reduced photosynthesis due to an O_3 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 O_3 effects on plant growth and reproduction. In particular, O_3 exposure has been shown to reduce the allocation of carbohydrate from shoots to roots and thus lower the root/shoot biomass ratio (fraction of total biomass in root tissue) (Cooley and Manning 1987), an effect that may have wider implications for below ground processes in the plant's environment (see Sect. 5.2) Several recent meta-analyses have summarised the available information across various types of plants (trees, crops, grassland and native species) and O_3 exposure conditions (Morgan et al. 2003; Grantz et al. 2006; Wittig et al. 2009; Wang and Taub 2010). For example, according to the literature compilation of Grantz et al. (2006), who used a root:shoot allometric coefficient k, which is the relative ratio growth rate of the root and shoot, to describe O_3 effects, O_3 reduced k on average by 5.6 %. Out of 125 observations of changes in k, 55 % yielded a decrease in k. However, about a third of all observations yielded an increase in k. Wang and Taub (2010) examined root mass fraction (i.e. the fraction of root to total biomass) of mostly herbaceous and a few woody species and found that, on average, O_3 reduced biomass allocation by 8.5 %. Wittig et al. (2009)

focused on tree species only and concluded from their analysis that the root-to-shoot ratio indicated a greater sensitivity to O_3 than shoot production. Their results also pointed to a greater sensitivity of angiosperm species in comparison to gymnosperms, which may have wider implications for community persistence (see Sect. 5.3). On the other hand, there are also reports of positive O_3 effects on root biomass production and root-to-shoot ratios especially in tree species (Pregitzer et al. 2008; Matyssek et al. 2010a, b). Overall, although the results of the majority of investigations point to a reduction of carbon allocation to roots, there is still uncertainty as such an effect depends on the respective O_3 concentration, the duration of exposure, the plant species or genotype, respectively, and on modifying factors of other growth variables. For example, already Maurer and Matyssek (1997) pointed out that the outcome of an O_3 effect on the root/shoot ratio of birch trees may be co-determined by the nutritional status of the respective plants.

There has been clear evidence over the last years that exposure to O_3 decreases growth in numerous plants representing important species of agro- and forest ecosystems as well as of different natural ecosystems. Wittig et al. (2009), for example, analysed growth responses of forest species from 263 studies over the past 40 years and found that elevated O_3 concentrations (97 ppb) decreased annual total biomass growth by 11–17 %. The decreased effect at current ambient concentrations as reported in these studies was 7 %. Detrimental O_3 effects on growth and yield of the major global food crop species, such as wheat, rice, soybean and cotton, have repeatedly been described (e.g. Heagle 1989; Morgan et al. 2003; Fiscus et al. 2005; Ashmore 2005; Ainsworth 2008; Booker et al. 2009). Mills et al. (2007) analysed O_3 exposure-response data for 19 agricultural and horticultural crops, respectively, and identified wheat, water melon, pulses, cotton, turnip, tomato, onion, soybean and lettuce as the most O_3-sensitive crops, while, for instance, barley was classified as O_3 resistant. Morgan et al. (2003) calculated an average yield loss of soybean of 24 % compared to charcoal-filtered air with small losses (approx. 8 %) at low (30–60 ppb) and high losses (approx. 35 %) at high (80–120 ppb) O_3 concentrations when they compiled 53 studies which included chamber and open-air O_3 exposure studies. Feng et al. (2008) calculated yield losses of winter and spring wheat ranging from 20 % at 42 ppb (7-h daily average) to 60 % at 153 ppb. According to a review of rice studies by Ainsworth (2008), average rice yields declined by 14 % when exposure to O_3 at a concentration of 62 ppb was compared to charcoal-filtered air. Despite this evidence of negative O_3 effects, one of the most common observations in studies with crop species is that there is considerable genotypic variability in O_3 sensitivity, suggesting that there is potential to breed for O_3 tolerance (Ainsworth et al. 2008; Booker et al. 2009). Production of biomass in grassland or pasture plants can also be negatively influenced by O_3 (Fuhrer 1997, 2009), but for species grown in mixtures other endpoints than biomass growth such as seed output or species composition may be important (see Sect. 5.3).

Studies conducted during the last three decades have repeatedly demonstrated that various stages of reproductive development are clearly sensitive to O_3. A recent meta-analysis of O_3 effects on reproductive growth and development of various plant species indicated that current ambient O_3 concentrations significantly reduced seed number, fruit number and fruit weight, while there was a trend towards increasing flower number and flower weight at elevated O_3 (Leisner and Ainsworth 2012). Negative effects on the reproductive performance in response to O_3 may result from a reduction in plant growth, a decreased reproductive allocation or from direct effects on reproductive structures (Black et al. 2000). Bender et al. (2006a) observed contrasting effects on resource allocation to the vegetative and reproductive organs of 17 herbaceous species that were exposed to different O_3 regimes from the seedling stage to the flowering stage. Although O_3 caused comparable reductions in both vegetative and reproductive growth in the majority of the investigated species, three species (*Chenopodium album*, *Matricaria discoidea*, *Stellaria media*) showed a greater vegetative growth and reduced reproductive allocation. Germinability of the seeds was affected by O_3 such that germination rate was up to 30 % lower in O_3-treated plants compared to control plants (Bender et al. 2006a). Similarly, Darbah et al. (2008) investigated the effects of elevated O_3 on reproductive fitness in paper birch (*Betula papyrifera*) under free air O_3 exposure. Elevated O_3 increased flowering, but decreased seed weight and germination rate. These results suggest that O_3 can significantly affect resource allocation patterns and reproductive fitness which may have significant implications for the establishment and survival of the progeny and hence for plant productivity and composition of plant communities under the influence of O_3 (see Sect. 5.3).

Any impact of O_3 exposure on the timing of flowering may also play an important role in reproductive success, particularly for species in which flowering is closely synchronised with pollinating species (Black et al. 2000; Hayes et al. 2012). However, the impact of O_3 on the timing of flowering varies markedly between species. Such O_3 effects have particularly been investigated in herbaceous species of grassland and ruderal ecosystems. For example, O_3 exposure has been reported to delay flowering in two species (*Campanula rotundifolia* and *Vicia cracca*) of simulated meadow community mesocosms (Rämö et al. 2007). In mesocosms representing “calcareous grassland”, O_3 has been found to accelerate the timing of the maximum number of flowers in *Lotus corniculatus* (Hayes et al. 2012). By contrast, Bergmann et al. (1996) showed that the timing of flowering and seed set in 17 wild plant species were not significantly influenced by season-long exposure to 1.5 × ambient O_3 concentration in OTCs. However, O_3-induced changes in flowering timing could have large ecological impacts on plant pollination and the food supply of nectar feeding insects.

4.5 Abiotic and Biotic Factors Modifying O_3 Responses

There are complex interactions between O_3 effects on plants and other abiotic and biotic factors, as O_3 effects may be modified by these factors or O_3 itself may modify plant responses to these other factors. Important abiotic modifiers are temperature, humidity, light, water and nutrient availability, the occurrence of other air and soil pollutants and altered atmospheric chemistry (e.g. CO_2 concentration). On the other hand, biotic factors that interfere with O_3 effects are insect pests and other diseases or pathogens and root microorganisms, resulting in either detrimental biological effects or mutually beneficial relationships (e.g. root nodulation by Rhizobium; mycorrhizal infection). There is a very large body of previous information ranging from controlled environment to field experimentation that has investigated these interactions. Although these modifying factors may be of particular relevance for an assessment of O_3 cause–effect relationships at the ecosystem level, the vast scope of their possible interactions cannot be listed here in detail. Rather, we will provide a brief summary evaluation on important modifying factors of O_3 effects based on recent studies.

Light, temperature and air humidity are prominent abiotic factors that interfere with O_3 effects. Increased light intensity has been claimed to increase the sensitivity to O_3 of light-tolerant species while decreasing that of shade-tolerant species; this assumption has many exceptions (Topa et al. 2001). While previous studies revealed little modifying influence of temperature, some recent field studies have indicated that O_3 impact significantly increases with increased ambient temperature (Mills et al. 2000). On the other hand, there is no new evidence to contradict that O_3 enhances the sensitivity of plants to low temperature stress. It is also known that air humidity enhances the adverse effects of O_3 by affecting stomatal conductance and thereby increasing O_3 flux into the plant. For the current understanding of $O_3 \times$ drought interactions refer to Sect. 4.2.

It has also long been known that the nutritional status of plants can influence its response to O_3; however, the interaction of O_3 with specific nutrients is still contradictory. While some experiments point to higher sensitivity towards O_3 under low nutrient supply, other research results with trees suggest that O_3 and nutrient supply do not interact. With respect to forest and other nutrient poor ecosystems, the co-occurrence of nitrogen (N) deposition and O_3 impacts are of particular concern. Generally, existing information including several more recent studies with tree (Handley and Grulke 2008; Thomas et al. 2006; Watanabe et al. 2007) and pasture species (Bassin et al. 2007b; Volk et al. 2011; Wyness et al. 2011) shows that the interactive effects of N deposition and O_3 vary among species and ecosystems, i.e. there is no consistent information whether N deposition either enhances O_3 toxicity or increases tolerance of plants towards O_3 stress. There are hardly any recent studies on interactions of other air pollutants such as sulphur dioxide or nitrogen oxide with O_3.

Along with the increasing concern about climate change effects on ecosystems during the last decades, research into O_3 interactions particularly with elevated atmospheric CO_2 concentrations [eCO_2] has increased (Fuhrer 2003; Paoletti and Grulke 2005; Lindroth 2010). As [eCO_2] is known to stimulate photosynthesis, to decrease stomatal conductance and mostly to enhance plant growth, while O_3 has negative impacts on photosynthesis and plant growth, interactions between the two gases can be expected. Consistent across different vegetation types and derived from various experimental approaches, there is evidence that [eCO_2] has the potential to mitigate negative effects of O_3, mainly due to a CO_2-induced reduction in stomatal conductance, which reduces O_3 uptake. On the other hand, negative O_3 effects limit positive responses to [eCO_2] in many plants as well (Fiscus et al. 2005). While the $CO_2 \times O_3$ interaction is of little relevance for the current ambient conditions, it may be suggested that the continuing future increase of the CO_2 component of climate change may be ameliorative for the effects of O_3.

Among the interactions of O_3 with biotic factors, plant pathogens and insect pests have repeatedly been studied in various experimental approaches (Percy et al. 2003a, b; Eastburn et al. 2011). While it may be assumed that reduced plant vigour due to O_3 stress can make plants more susceptible to plant pathogens, general predictions of O_3 effects on particular plant–pathogen systems are difficult to make, because the available data for specific pests and diseases remain controversial. With respect to agricultural plants there is no fundamentally new recent information to replace the summary by Manning and von Tiedemann (1995), that increased susceptibility after O_3 exposure can be expected for necrotrophic pathogens, while obligate biotrophic infections tend to be diminished by O_3.

Insects can respond to O_3-induced changes in the plant chemical composition or insect performance is directly affected by O_3. Overall assessments and some more recent studies, respectively (Holopainen 2002; Valkama et al. 2007; Bidart-Bouzat and Imeh-Nathaniel 2008; Lindroth 2010), can be interpreted that an O_3 exposure may increase the likelihood and success of chewing insect attacks. Existing studies on interactions of O_3 with sucking insects such as aphids do not allow to deduce consistent trends. Among the aspects of the many other biotic factors that interact with O_3 or which modify plant O_3 responses, respectively, symbioses with mycorrhizae and plant–plant interactions by competition are partly addressed in Sects. 5.2 and 5.3.

5 O_3 Impacts at the Ecosystem Level

The recent emphasis of the importance of ecosystems for the functioning of the biosphere and their role in providing goods and services to humans has resulted in various attempts to assess the role of O_3 at the ecosystem scale (MEA 2005). However, ecosystem effects of O_3 are difficult to detect and to evaluate, as the different systems vary at spatial and temporal scales. With the exception of two recent multi-year field experiments in a rapidly growing tree plantation (Karnosky et al. 2001) and in an adult forest tree stand (Matyssek et al. 2013), the number of studies at the scale of forest-, agro- or grassland ecosystems especially under exposure to O_3 over several growing seasons is still very limited, which is even more true for other types of vegetation like fens, bogs, etc. The following section will consider selected examples where O_3 effects may be relevant in an ecosystem context (Fig. 4).

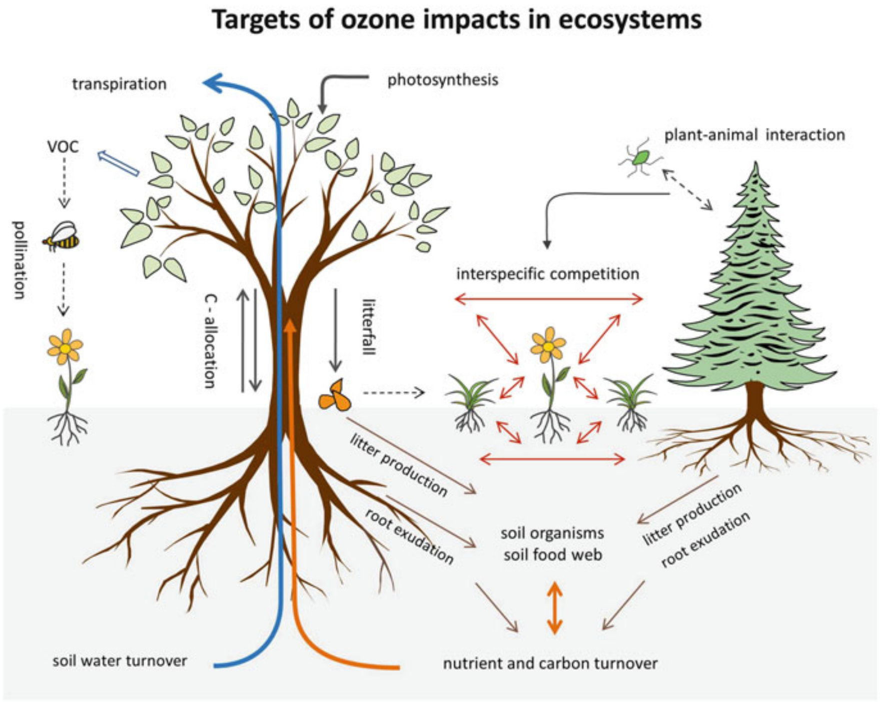

Fig. 4 Schematic representation of structural elements and processes in ecosystems that are potential direct and indirect targets of an O_3 exposure and which are partly described in the text

5.1 *Effects on Water Relations and Hydrology*

As shown in Sect. 4.1, the main route of entry of O_3 into the plant interior is via stomatal uptake at the leaf level. This role of the stomata has also been proofed at larger scales. For example, previous studies of Duyzer et al. (1995) in forest ecosystems have demonstrated that O_3 deposition is related to g_s at the stand level. However, as O_3 effects on g_s have been variable (Sect. 4.2), there remains uncertainty with respect to O_3 responses of water use at the canopy or stand level.

Investigations with tree species under open-air O_3 exposure conditions using sap flux measurements have shown that stand level water use per unit ground area of aspen clones was not significantly affected by elevated O_3 although the treatment decreased leaf area index by 22 % and basal area by 20 % (Uddling et al. 2008). Uddling et al. (2009) attributed this to an increased leaf area-specific hydraulic conductance. The O_3 effect was assumed to be caused by the sluggish stomatal response (Sect. 4.1), as under O_3 exposure the stomatal closure response to increasing vapour pressure deficit was less sensitive than under the control treatment. Moreover, mid-day leaf water potential was more negative under elevated O_3 compared to controls. The lack of an O_3 effect on stand-level water use may also be caused by a higher proportion of sun leaves in trees under elevated O_3 compared with control trees (Uddling et al. 2008). Also, in an experiment with aspen and birch, Rhea et al. (2010) found that O_3 changed the branch architectural parameters, which may alter tree crown interception of precipitation and thus affect evapotranspiration.

Field studies in a deciduous forest in eastern Tennessee provided some insight into the possible consequences of stomatal sluggishness at the leaf level for ecosystem water cycling (McLaughlin et al. 2007a, b). It was found that daily O_3 levels with maxima ranging from 69 to 82 ppb reduced stem growth by up to 50 % in 1 year with high O_3 levels. The authors suggested that peak hourly O_3 exposures resulted in an increase of the rate of water loss through transpiration as indicated by an increased stem sap flow. Due to the increased canopy water loss water uptake by the trees increased as reflected in reduced soil moisture in the rooting zone. At the landscape level this change in tree water use was assumed to lead to further impacts on the hydrological cycle and O_3 has been reported to contribute to variation in late-season streamflow by as much as 23 % in areas of highest exposure in forested watersheds in Tennessee (Sun et al. 2012). A loss in stomatal sensitivity associated with increased evapotranspiration and reduced streamflow can be expected to increase drought episodes and to have implications for flow-dependent aquatic biota (Sun et al. 2012). Recent studies with several crops and grassland species have also indicated an O_3-induced loss of stomatal sensitivity to drought, light and vapour pressure deficit (Wilkinson et al. 2012; see Sect. 4.2), but the implication of these observations on individual plant species for intact agro- and grassland ecosystems remains unclear.

Although there is no clear pattern of the impact of O_3 on stomatal functioning (see Sect. 4.2), recent ecosystem models that address the larger scale effects of O_3 on water turnover are often based on the assumption that O_3 induces a stomatal closure. For example, in order to assess the interactions of O_3, climate, elevated CO_2 and N limitation on the hydrological cycle in the eastern USA, Felzer et al. (2009) used the terrestrial ecosystem model TEM-Hydro. According to this model elevated CO_2 decreased evapotranspiration by 2–4 % and increased runoff by 3–7 %, as compared to the effects of climate alone. Including O_3 damage and N limitation into the calculations, evapotranspiration was reduced by an additional 4–7 % and runoff was increased by an additional 6–11 %. Hanson et al. (2005) using a stand-level simulation model found a modest 3 % reduction in water use when the O_3 concentration was raised by about 20 ppb above the prevailing ambient level.

5.2 Below-Ground Effects

Atmospheric ground level O_3 exposure does not directly affect structural and functional soil properties. However, above- and below-ground processes are interconnected via plant shoot and root communication mediated by the flow of carbon (see Sect. 4.4). Consequently, any O_3-induced alteration of the quantity and quality of carbon supply from either photosynthates or from litter fall to the soil or from an enhanced carbon allocation to above-ground processes due to an O_3-induced stimulation of the production of antioxidants and other chemical compounds for defence and repair processes may exert indirect O_3 effects on the soil system (Cooley and Manning 1987; Andersen 2003; Pregitzer and Talhelm 2013). Moreover, reduced biomass allocation to roots may lower the water availability to plants, which feeds back to stomatal conductance, canopy water flux, hydrology (Sect. 5.1) and nutrient cycling. Examples of O_3 effects on the soil system include changes in litter quality and consequences for various soil biota. Additional effects like alterations of soil carbon formation and of decomposer activities as well as of soil food web structures are not considered here.

Modification in the quality of litter (e.g. soluble sugars, tannins, phenolics, lignin, macro- and micronutrients) released from plants exposed to O_3 have repeatedly been observed. In their review Kasurinen et al. (2007a) concluded from existing information with boreal and temperate forest trees that O_3 effects on litter chemistry were mostly observed only at high O_3 concentrations. For example in an OTC study with birch (*Betula pendula*) clones O_3 slightly increased the content of leaf low molecular weight phenolic compounds, an effect which did not persist over the 3-year study. On the other hand, litter chemistry was not affected by short-term O_3 exposure in a study with beech *Fagus sylvatica* (Schloter et al. 2005). In free air type O_3 exposure experiments, it has been demonstrated that O_3-induced changes in litter quality of *Populus tremuloides* and *Betula papyrifera* communities led to reduced inputs of hemicellulose and lignin (Liu et al. 2005; Meehan et al. 2010) and thus caused a decrease in nutrient flux into soil (Liu et al. 2007). In contrast, Stoelken et al. (2010) detected additional nitrogen incorporation into the soil down to 30 cm resulting from an enhanced nitrogen mobilisation from leaf litter in an O_3 exposure experiment with *Fagus sylvatica* grown in lysimeters.

Ozone effects on soil biota have received more recent attention especially with respect to possible implications for soil biodiversity; however, there is little evidence from experimental studies in real ecosystems with their respective native soil properties. Effects of O_3 on the soil microbial community have been investigated both in the rhizosphere and in the bulk soil of trees, grassland and arable crop species.

In an OTC study with potted plants total bacterial biomass was decreased by O_3 in the soil of the N_2-fixing herbaceous legume *Lathyrus pratensis*, but not in the soil of the grass *Agrostis capillaris* (Manninen et al. 2010). In a multi-year mesocosm study with *Pinus ponderosa*, elevated O_3 tended to increase the ratio of fungal to bacterial biomass (Olszyk et al. 2001) and such an effect was also observed under similar O_3 exposure conditions for blue wildrye (*Elymus glaucus*, Yoshida et al. 2001). For the tree species *Fagus sylvatica*, a shift in the overall community structure of soil microorganisms based on phospholipid fatty acids (PLFA) analysis as a biomarker in response to O_3 (Pritsch et al. 2009) has been found to be associated with a reduction in the potential nutrient turnover (Schloter et al. 2005) and a higher abundance of plant-carbon utilising microbes (Esperschutz et al. 2009).

Aneja et al. (2007) characterised the diversity of microbial communities colonising control and O_3-exposed litter from *Fagus sylvatica*/*Picea abies* and provided evidence that changed litter quality due to elevated O_3 influenced the structure of litter-colonising microbial communities. In peat-land microcosms (*Eriophorum vaginatum*), Morsky et al. (2008) found an O_3-induced increase in microbial biomass only at the end of a 3-year exposure experiment, a result which supports the conclusion of Kasurinen et al. (2007a) that the onset of microbial responses due to an O_3 impact may take years.

Dohrmann and Tebbe (2005) studied the rhizosphere bacterial community composition of five low-managed grassland species using genetic profiling of PCR amplified 16S rRNA gene sequences based on single-strand conformation polymorphism (SSCP). They found that a 5-week exposure to elevated O_3 did not select for a different bacterial community composition. This was also true if other more O_3 susceptible herbaceous plant species with severe visible O_3 injury were studied (Dohrmann and Tebbe 2006). Also with a grassland system Kanerva et al. (2008) in a 3-year O_3 exposure study provided evidence that elevated O_3 is able to modify the structure of the microbial community in a meadow soil, as bacterial, actinobacterial and fungal PLFA biomass were decreased simultaneously. Again this study points to the fact that long-term observations are necessary to understand the effects of O_3 on the biology of soil processes in ecosystems.

Because of its implication for nutrient acquisition, *mycorrhization* is of high importance for ecosystem function. An ectomycorrhizal community responded to changes in environmental conditions with a change in its total amount of extramatrical mycelium, leading to changes in space occupation, and consequently, to alterations in its capacity to exploit soil resources (Agerer et al. 2012). Several recent studies described effects on mycorrhizal abundance when host trees were exposed to O_3. For example, for *Betula pendula* Kasurinen et al. (2005) found a stimulation of total mycorrhiza infection, Haikio et al. (2009) an increased mycorrhizal status for hybrid aspen (*Populus tremula* L. *x Populus*) and Pritsch et al. (2009) and Grebenc and Kraigher (2007a) a higher total number of mycorrhiza types under OTC and free air O_3 exposure conditions. For ectomycorrhizae collected underneath mature Norway spruce trees at the “Kranzberger Forst” free-air O_3 fumigation site, differences in carbon allocation to the mycorrhizal communities have been shown between the different O_3 treatments by means of differences in the enzyme activity profiles of the ectomycorrhizae communities (Agerer et al. 2012). Moreover, there is past and recent evidence from studies with tree species that O_3 impacts the microbial diversity also in terms of mycorrhizal species composition as shown for *Pinus taeda* (Edwards and Kelly 1992), *Betula pendula* (Kasurinen et al. 2005), *Fagus sylvatica*, (Haberer et al. 2007; Grebenc and Kraigher 2007b) and for an aspen and aspen-birch community in a free air O_3 exposure experiment (Edwards and Zak 2011). On the other hand, data about O_3 effects on the mycorrhization of grassland and other crop species are limited. The mycorrhizal colonisation of blue wildrye (*Elymus glaucus*) was reduced in response to O_3, and it has been demonstrated that this effect depends on the genotype of the grass tested (Yoshida et al. 2001).

Until now few studies have addressed possible implications of plant exposure to O_3 for detritivore invertebrate communities and particularly soil mesofauna composition which are important for ecosystem functioning. In a free air O_3 exposure experiment with temperate forest tree species (aspen and aspen-birch communities) the individual density of soil mites was reduced by nearly 50 % under elevated O_3 conditions, whereas the abundances of collembolans remained unchanged (Loranger et al. 2004). Feeding experiments with litter with altered quality due to previous O_3 exposure of trees were able to demonstrate that growth rates were reduced for the earthworm (Lumbricus terrestris) fed with birch litter (Kasurinen et al. 2007b) or for a collembolean species fed with aspen litter (Meehan et al. 2010). With regard to arable agroecosystems Schrader et al. (2009) observed a decrease in the individual density of enchytraeids, collembolans and soil mites in the rhizosphere of O_3-exposed wheat plants in OTCs and Chang et al. (2011) found a reduction in the abundance and diversity of collembolans associated with cotton plants exposed to O_3. Overall, these few selected examples clearly show that the above-ground impact of O_3 on plant performance may translate into significant secondary below-ground implications in the ecosystem.

5.3 Plant Competition and Community Composition

Driven by concerns about the global changes in biodiversity and the well-known fact that plant growth responses to O_3 vary significantly between species and genotypes, an arising question is whether exposure of vegetation to high levels of O_3 may alter the strength of competitive interactions between different plant species and whether this may lastly result in changes of plant community composition. The way by which elevated levels of O_3 will shape the composition includes a change in the cover or abundance of single plant species, which in turn will change the genetic structure of the community. The challenge to describe O_3 risks on plant communities is the understanding of how competitive interactions may modify growth responses of individual species to O_3 and, conversely, how the impact of O_3 may modify their competitive ability within a plant assemblage. Research on this issue comprises both, experiments with older, established ecosystems and artificially newly created plant communities with the majority of experiments designed to study two-species mixtures or model plant communities under laboratory and field conditions.

Artificial forest communities have been investigated under laboratory and field conditions. Phytotron studies to test O_3 effects on the competition between *Fagus sylvatica* and *Picea abies* revealed that the responses to O_3 strongly depended on the type of competition: although the response to O_3 of *P. abies* was not significantly affected by either intra- or interspecific competition, the competitive ability of this species was scarcely affected by O_3 as indicated by an enhanced above-ground growth of the competing *F. sylvatica* plants (Grams et al. 2002; Kozovits et al. 2005). Under conditions of interspecific competition, *P. abies* was found to be superior in nitrogen acquisition whereas *F. sylvatica* in turn appeared to be nitrogen-limited (Grams and Matyssek 2010; Kozovits et al. 2005). Effects on nutrient efficiency indicate that processes of stress defence due to O_3 exposure trigger a nutrient demand at the expense of above-ground competition (Rodenkirchen et al. 2009). Recently, Grams et al. (2012) demonstrated that the more intense the competition between *F. sylvatica* and *P. abies* is, the stronger the response to other stressors may be modified.

Under free air O_3 exposure conditions, stands of different clones of *Populus tremuloides* (aspen) or mixed stands with either *Betula papyrifera* or *Acer saccharum* were investigated during a 12-year experiment. The growth response of *P. tremuloides* depended on clone and competitive status (Kubiske et al. 2007; McDonald et al. 2002). After 7 years of exposure, O_3 slightly enhanced the rate of conversion of a *P. tremuloides* stand to a *B. pendula* stand (Kubiske et al. 2007), whereas the cumulative nitrogen-acquisition decreased in both species (Zak et al. 2007). When the experiment went on for 12 years, the rank order of nitrogen-acquisition among *P. tremuloides* genotypes was not shifted over time, indicating no change when juvenile trees mature (Zak et al. 2012).

In the above experiment an understory community established which consisted of more than plant 30 species dominated by perennial old field vegetation. Observed effects on total and individual species biomass, N content, and ^{15}N recovery of this understory vegetation could not be related directly to the O_3 treatments but rather reflected the effects on the structure of the overstory community, which is determined by the present tree species and their response to the treatments (Bandeff et al. 2006).

Ozone effects on established forest plant communities have already been assessed in some earlier studies. For example, Nygaard (1994) and Steubing et al. (1989) investigated the responses of understory species growing in an intact conifer or beech forest, respectively, to relatively high O_3 exposures and found high variability between species in O_3 sensitivity. Barbo et al. (1998) examined the response to sub-ambient and enhanced O_3 levels of an early successional plant community associated with *Pinus taeda*. In this study, O_3 exposures caused shifts in the competitive interactions between plants and the abundance of the five most common species was affected already in the first year. The authors concluded that total vegetative cover, vertical density of foliage as well as species richness, diversity and evenness may be at risk by the prevailing ambient O_3 exposures.

A group of beech and spruce trees within a 55-year-old Norway spruce stand (Kranzberger Forst, Germany) has been exposed for 8 years to enhanced O_3 levels using a newly developed free-air O_3 fumigation system (Matyssek et al. 2010a, b, 2013). One of the results showed that individuals of both tree species, spruce and beech, grew faster in mixture than in pure stands reflecting a facilitation of spruce and a reduction in competitiveness of beech. The results of this research project led to the conclusion that increasing levels of O_3 stress may change the pattern of carbon allocation in mixed stands of beech and spruce and the outcome of competition (Pretzsch and Schutze 2009). Actually, Pretzsch et al. (2010) demonstrated a shift in the resource allocation in mature trees caused by exposure to high O_3 levels.

In comparison to studies with forest plants, a much large number of more recent studies on O_3 effects on plant competition are available for grassland communities. This may be due to the fact that a generally accepted outcome of screening experiments with single plants or monocultures is that members of Fabaceae (legumes) with the genus *Trifolium* in particular belong to the most O_3-sensitive plant species, whereas members of the family Poaceae are much less responsive to O_3 (Fuhrer 1997). Experimental approaches to address O_3 effects on interspecific competition between herbaceous plant species have thus focused on grass/clover mixtures.

With respect to artificial grassland communities, more recent experiments with potted plants of artificial grass/clover mixtures confirm earlier results such that markedly negative growth response of the clover to O_3 exposure is observed, whereas the grass species were hardly impaired by O_3 (González-Fernández et al. 2008; Haldemann and Fuhrer 2005; Hayes et al. 2009, 2010a). If the total biomass of the species mixture was largely influenced by the more sensitive component, a decline in total yield of the mixture has been recorded under O_3 exposure (e.g. for *Trifolium repens*/*Lolium perenne*, Hayes et al. 2009; for *Trifolium pratense*/*Trisetum flavescens*, Nussbaum et al. 2000). On the other hand, a range of O_3 exposure experiments resulted in unchanged total yield quantities (e.g. for *Trifolium repens*/*Lolium perenne*, González-Fernández et al. 2008; or grass/alfalfa, Johnson et al. 1996). This result derives from the fact that an O_3-induced decline in the relative yield of clover entailed an increase in the relative yield of the grass component. In addition, it has been argued that altered root/shoot ratios (Haldemann and Fuhrer 2005) and reduced remobilisation of reserves after grazing (Nussbaum et al. 2000) due to the O_3 impact could facilitate the less sensitive species. Thus, O_3 may interact with cutting or grazing by reducing the capacity for regrowth from energy reserves (Ashmore and Ainsworth 1995). It should be mentioned that these recent findings from experiments using potted plants had already been observed with similar tendencies in older field experiments with natural grass/clover communities, where plants were exposed to O_3 under OTC conditions (Blum et al. 1983; Rebbeck et al. 1988; Heagle et al. 1989).

There is also recent evidence that the presence of an interspecific competitor (grass) may affect the response of the clover species to O_3. In two-species mixtures, adverse effects of O_3 on productivity may be enhanced by competition as shown for *Trifolium pratense* in competition with *Trisetum flavescens* (Haldemann and Fuhrer 2005) or mitigated by competition as shown for *Trifolium repens* in competition with *Lolium perenne* (González-Fernández et al. 2008).

Ozone effects on plant competition of two-species mixture have recently also been investigated without legumes. Using a phytometer approach, the response of early season O_3 stress on model communities of wet grassland species (Tonneijck et al. 2004) and ten different extensively managed grassland species (Bender et al. 2002, 2006b) was investigated over three seasons under OTC conditions with moderately enhanced O_3 levels. In the latter studies, for none of the ten species O_3 impacts on growth were detected when grown in monoculture. Target species differed significantly in their competitive ability against the phytometer (*Poa* *pratensis*) but the experiments did not provide evidence that interspecific competition altered the harmful effects of an early season O_3 stress on aboveground growth. Only for *Veronica chamaedrys*, O_3 was shown to affect its competitive ability against *Poa pratensis* negatively (Bender et al. 2002, 2003). A similar increase in the grass cover ratio under O_3 exposure was demonstrated for *Anthoxanthum odoratum* and *Dactylis glomerata*, respectively, when grown in competition with *Leontodon hispidus* (Hayes et al. 2011).

In previous studies with artificial pasture model plant communities composed of grasses, clover and weeds, the decline in the clover component, *T. repens* and/or *T. pratense* due to the O_3 impact, was associated with a slight increase in the yield of grasses (e.g. field-sown, Fuhrer et al. 1994 and pot-sown, Ashmore et al. 1996). Conversely, in a simulated community representing a typical multi-species UK upland grassland, the grass *Anthoxanthum odoratum* was most affected by an experimental O_3 exposure in terms of aboveground biomass reduction and this effect contributed to a decrease in total community biomass and grass:forb ratio (Hayes et al. 2010b). In Finland, in a study with meadow species in mesocosms, after only 2 years of moderate exposure to O_3, the early season coverage of plant communities was decreased (Rämö et al. 2007); however, the reductions in aboveground biomass were not reflected in changes in the dominance of different functional groups or in the total community root biomass (Rämö et al. 2006).

There are also reports that describe modifying effects of plant competition in grassland communities on the impact of O_3 on plant flowering and visible leaf injury. Among characteristic species of therophytic dehesa grasslands, flower production of *Trifolium cherleri*, *Trifolium subterraneum* and *Trifolium striatum* was suppressed by O_3 in competition with the grass species *Briza maxima*, but there was no interaction between competition and O_3 response (Gimeno et al. 2003). In a complex grassland model community, the timing of flowering and the number of flowers of *Lotus corniculatus* were accelerated by O_3, while a significant reduction in the numbers of flowers with increasing O_3 levels was found for *Campanula rotundifolia*, *Scabiosa columbaria* and *Vicia cracca* (Hayes et al. 2012; Rämö et al. 2007). Such changes in timing and number of flowers could have implications for pollination and the long-term outcome of the whole community development. Reduced proportions of injured leaves on O_3 exposed grasses due to the presence of a competitor have been described. For example, *Trisetum flavescens* responded more strongly in mixture with the low stature species *Centaurea jacea* than in mixture with *Trifolium pratense* (Nussbaum et al. 2000). Similarly, *Leontodon hispidus* exhibited a larger increase in O_3-induced senescence observed in the more open canopy of *A. odoratum* compared to the denser canopy of *D. glomerata* (Hayes et al. 2011). Modification of microclimate and canopy structure are thought to be potential mechanisms that influence the interaction between O_3 responses and competition (Haldemann and Fuhrer 2005; Hayes et al. 2010a).

Investigations on O_3 effects on older, established communities of managed and semi-natural grassland have been done in several earlier and more recent studies (Table 2) and will be discussed here in more detail. For example, Nebel and Fuhrer (1994) classified 31 species according to the appearance of visible injury when

Table 2 Effects of O_3 exposures on species composition in experiments with established grassland communities

Community	Main species	Exposure	Effect on species composition	References
Mesotrophic grassland	*Festuca rubra* *Bromus erectus* *Filipendula vulgaris* *Pimpinella saxifraga* *Arrhenatherum elatius* *Dactylis glomerata* *Holcus lanatus*	OTC	Trends of changes in species composition Shift towards a more calcareous grassland community	Ashmore et al. (1995)
Semi-natural chalk grassland	*Festuca rubra* *Campanula rotundifolia* *Galium verum* *Plantago lanceolata* *Festuca rubra* *Arrhenatherum elatius* *Bromus erecta* *Poa pratensis* *Dactylis glomerata*	OTC	Consistent decline in cover of *F. rubra* *C. rotundifolium* was lost from all ozone treatments Increase in frequency of G. verum Increase in frequency of P. lanceolata	Thwaites et al. (2006)
Low managed grassland Geo-Montani-Nardetum (Alp Flix)	*Festuca violacea Nardus stricta Carex sempervirens Ranunculus villarsii Leontodon helveticus Ligusticum mutellina Potentilla aurea*	Free air	No effects on the abundance of the most frequent species	Bassin et al. (2007b)
Semi-natural grassland Arrhenatheretum elatius-Festuca rubra subcommunity	*Agrostis capillaris* *Festuca rubra* *Poa pratensis* *Veronica chamaedrys* *Trifolium repens* *Plantago lanceolata* *Stellaria graminea*	OTC	No change in species richness Effect on the proportion of grass to forb cover values *T. repens* and *V. chamaedrys* increased in cover *A. capillaris* decreased in cover	Evans and Ashmore (1992)

(continued)

Table 2 (continued)

Community	Main species	Exposure	Effect on species composition	References
Arrhenatherion elatioris Low-to-medium productivity 30-year–old field (Le Mouret)	*Bromus hordeaceus* *Holcus lanatus* *Trisetum flavescens* *Alopecurus pratensis* *Arrhenatherum elatius* *Plantago lanceolata* *Ranunculus friesianus* *Trifolium pratense*	Free-air	Change in fraction of functional groups Legume fraction shows a negative response Negative effects of ozone on grass and legume fraction No response of the forb fraction	Volk et al. (2006) Stampfli and Fuhrer (2010)
Mesotrophic grassland	*Festuca rubra* *Holcus lanantus* *Anthoxanthum odoratum*	Free-air	Influence on the composition of the herb and legume group	Wedlich et al. (2012)

grown in soil blocks of intact semi-natural grassland vegetation and Evans and Ashmore (1992) showed that during a season with relative high O_3 levels total aboveground biomass of a semi-natural grassland community was decreased. More recently, an old, species-rich (53 species) pasture at a mid-elevation site in Switzerland was exposed for seven years to O_3 in a free air exposure system under real field conditions (Volk et al. 2003). For individual growth periods, no relationship between the O_3 exposure level and yield differences was observed. After 5 years a loss in annual dry matter yield of about 23 % was calculated for conditions of moderately elevated O_3 levels (1.5 × ambient air) showing a strong negative response of the yield of the fraction of legumes (Volk et al. 2006) but not of the frequency of legumes at the experimental plots (Stampfli and Fuhrer 2010). In a natural upland mesotrophic grassland in UK, Wedlich et al. (2012) revealed clear evidence for a cumulative effect of moderately elevated O_3 levels (free-air exposure) over time (3 years) on species biomass composition as there was a significant negative effect of O_3 exposure on herb biomass, but not on total grass or legume biomass suggesting that finally O_3 had become the dominant factor influencing species composition within the combined herb and legume component.

Particularly for semi-natural calcareous grassland, a shift in species composition has been recorded which was indicated either by a decline (e.g. of the dominant grass species *Festuca rubra* or *Campanula rotundifolia*) or an increase (*Galium verum* and *Plantago lanceolata*) in cover or frequency of species (Thwaites et al. 2006). Bassin et al. (2007b) concluded that in old, species-rich grassland communities, effects of elevated O_3 on the productivity and floristic composition seem to develop rather slowly, as evidenced from the lack of significant vegetation responses of the sub-alpine grassland community to the elevated O_3 treatment over 7 years (Bassin et al. 2013). With respect to species-specific traits Bassin et al. (2009) suggested that commonly used principles of functional growth analysis do not directly hold under the specific conditions of such plant communities. As a reason, an adaptation to oxidative stress of the alpine species was discussed to account for the low sensitivity in response to the chronic low-level O_3 exposure used in this experiment (Bassin et al. 2013).

In summary, the studies cited above indicate that current and future O_3 concentrations could affect natural and semi-natural grassland communities and point out that detrimental effects on species balance may occur. In clover:grass mixtures a shift in species composition is the predominant effect, favouring the tillering of the grass component, whereas the effect on the total forage yield seems to be determined by the susceptibility of the individual species. Experiments with newly established grassland communities indicate that nitrogen-poor meadows are potentially very sensitive towards an O_3 impact. Mesotrophic grassland communities are characterised by the occurrence of faster growing species which are known to be more susceptible to O_3 than the slower growing calcareous grassland species. The low susceptibility of old, species rich grassland communities to O_3 is linked to specific characteristics of these systems. Low productivity vegetation such as subalpine grassland is mainly composed of species with a stress-tolerant growth strategy, which have been considered relatively unresponsive to O_3 (Bassin et al. 2007a). Probably, the high genetic diversity and the large rooting system, which entails resources to allow repeated establishment of a new photosynthetic canopy are the basis for a large resilience against declining biomass production (Bassin et al. 2007a, b; Volk et al. 2011).

As already shown for grassland communities, any differential O_3 susceptibility between plant species in terms of growth or fitness may alter their competitive interactions. This may also be assumed for plant competition in agro-ecosystems and has been shown for crop–weed interactions. Unfortunately, overall knowledge about this issue is rather scarce. Ozone impacts on competition between crops and the C-4 weed *Cyperus esculentus* have been investigated by Grantz and Shrestha (2005, 2006) and Shrestha and Grantz (2005). Fruit productivity of *Lycopersicon esculentum* in competition with this weed was reduced under low and moderate O_3 levels, whereas the crop responded only to high O_3 levels in the absence of the weed (Shrestha and Grantz 2005). In competition with *Gossypium barbadense*, O_3 impacts were compounded by *C. esculentus* (Grantz and Shrestha 2005) suggesting that high O_3 concentrations appear to increase the competitiveness of the weed with respect to cotton (Grantz and Shrestha 2006). Grantz et al. (2010) thus assumed that it is more likely that the level of threat to agricultural production from *C. esculentus* may increase due to enhanced competition for edaphic resources driven by the O_3 impact. Pfleeger et al. (2010) observed the response of a plant community emerging from a farm soil over several generations. Individuals from some of the species appeared to be diminished in number by the third year, such as *Capsella bursa-pastoris*, *Erodium cicurtarium* and *Spergula arvensis*, while biomass decreased with increasing O_3 exposure. Changes in competitive interactions and community dynamics seemed to be an indirect effect of premature senescence of taller species by altering light availability.

5.4 Ecosystem Productivity

Ozone effects on plant vigour, water relations and soil processes may finally all contribute to altered net primary productivity which is one of the key characteristics of any ecosystem function and service.

Forest productivity is of particular interest not only for timber production but also due to its implications for the global carbon cycle and climate change. Current O_3 levels are considered an important stressor of over 30 % of the world's forests (IPCC 2007; Royal Society 2008) and also constitute a risk for forests in Europe (Ashmore 2005; Matyssek et al. 2008). Such assessments of O_3 effects on forest ecosystem properties are based on experiments and models, but still remain uncertain. For example, most experimental approaches addressing this question were carried out with seedlings or individual young tree species, therefore extrapolation to the results of mature forest stands is limited (Karnosky et al. 2007).

DeMarco et al. (2013) applied a generalised linear/non-linear regression model to assess cause–effect relationships between primary productivity of *Quercus cerris*, *Quercus ilex* and *Fagus sylvatica* and climate and pollutants including O_3 in Italy and concluded that O_3 did not significantly affect net primary productivity. But this conclusion must be viewed with caution, because the authors only considered the external O_3 concentration (as AOT40; accumulated hourly mean O_3 concentration above 40 ppb), i.e. the O_3 exposure in their model rather than the O_3 uptake into the plants, which is toxicologically relevant for any risk assessment. Ollinger et al. (1997) combined leaf-level O_3 response data from O_3 fumigation studies with a forest ecosystem model in order to simulate the effects of ambient O_3 on mature hardwood forests in the northeastern United States. The predicted declines in annual net primary production in this modelling study ranged from 3 to 16 %.

Information on O_3 effects on the productivity of natural and semi-natural vegetation are to a large extent represented by studies on grassland (Bassin et al. 2007a; Fuhrer 2009; see Sect. 5.3). As grasslands comprise a variety of habitats described as meadows and fens, as well as agricultural grassland used for grazing, albeit maintained to conserve species diversity, a general assessment of an O_3 impact on these ecosystem type is difficult. Although O_3 has been reported to decrease productivity in individual grassland species grown in simulated mixtures (see Sect. 5.3), the few experiments with established grassland ecosystems have shown that their net primary production is quite resilient to elevated O_3 (Thwaites et al. 2006; Volk et al. 2011).

Ozone effects on agroecosystem productivity at the field scale and related to this the consequences for regional and global yields and agricultural productivity, respectively, have been assessed by experimental field studies and by regression models using the O_3 dose–response functions derived from these experiments. The most prominent examples of this approach are the previous multi-site field studies in National Crop Loss Assessment Network in the USA (Heagle 1989) and in the European Open-top Chamber Network (Jäger et al. 1992), where various crop species were exposed to O_3 in OTCs. Data from these experiments have been used widely to develop O_3 exposure–response models which again formed the basis to estimate regional or global productivity losses (in terms of crop yields) caused by O_3 (Wang and Mauzerall 2004; van Dingenen et al. 2009). For example, yield losses of important US crops crop species (maize wheat, sorghum, soybean) were calculated to be in the range of approx. 10 % when exposed to an average O_3 concentration below 50 ppb (7-h day^{-1}) or when exposed to O_3 concentrations above 80 ppb (7-h day^{-1}) (Booker et al. 2009). According to Mills et al. (2007) more than 20 % of the European crop production area is at risk for yield losses of about 5 % at current O_3 levels. Also, mostly based on OTC studies considerable yield losses of crops in Asian countries like India, Pakistan (Wahid 2006) and China have been estimated (Cho et al. 2011). Aunand et al. (2000) estimate that yield losses of soybean and wheat may range between 20 and 30 % by 2020 in China. More recently, the only two free air O_3 exposure experiments with crops worldwide have similarly shown that modest enhancements of ambient O_3 concentrations (which ranged between 42 and 62 ppb) resulted in yield losses of 5–18 % for rice (Shi et al. 2009), 15–25 % for soybean (Morgan et al. 2006) and 10–35 % for wheat (Zhu et al. 2011). Overall, the above examples all provide reasonable evidence that the productivity of important agro-ecosystems are at risk from current and future O_3 exposure. From the perspective of the growing global population with ever increasing future needs for food supply, the estimated yield losses of these crops are of concern. However, there remains uncertainty with these estimates as they rely on exposures to the external O_3 concentration rather than on the actual O_3 uptake into the crops.

6 Conclusions

Globally there is widespread evidence that tropospheric O_3 concentrations tend to increase. There is also long-term evidence that O_3 is highly phytotoxic and that vegetation is at particular risk from this pollutant. Driven by concerns about the potential losses in food crop and timber productivity due to O_3 exposures the mode of action of O_3 on individual plant species has been studied intensively during the last decades. Consequently, we now have a reasonable understanding how plant metabolism, physiology and growth vigour is affected by this pollutant and evidence that O_3 exposure causes yield losses of crops and forest trees. More recently, along with overall concerns about the pressures on global ecosystems derived from land use, climate change and overexploitation, etc. emphasis on the importance of ecosystems for the overall functioning of the biosphere has raised new questions about the role of O_3 as an additional threat to that role of terrestrial ecosystems. Here we have highlighted O_3 effects on plant water relations and the possible consequences for the hydrology of whole ecosystems, the possible consequences of an O_3-induced alteration of the carbon transfer between above- and belowground plant parts for soil carbon and soil organisms and the potential role of O_3

as a driver of plant biodiversity in vegetation. It is evident that in comparison to the level of single plants much of the existing information that would allow us to assess O_3 effects at the ecosystem level is still missing and inconsistent.

From the perspective of ecosystem effects this is particularly due to a paucity of adequate research efforts to study O_3 effects at the system level. This is equally true for agro-, forest- and other semi(natural) or grassland ecosystems, albeit these different systems require to consider different time horizons to assess any risk from O_3 stress. While two recent large-scale O_3 experiments with a forest plantation and a mature forest stand applying free air O_3 enrichment techniques have provided important information on the multitude of potential O_3 effects at the system or stand level, we need more of such experiments. This holds true not only with respect to other forest ecosystems at other sites but similarly also for other types of natural or semi-natural vegetation such as, e.g. pastures and grassland, particularly with an increased emphasis on biodiversity issues under the impact of O_3. Also for agroecosystems where O_3 effects have almost always been considered under aspects of food security, the challenge remains to clearly demonstrate at the field level the "true" extent of either direct or indirect O_3 impacts on crop yield and quality. To address the various inconsistencies in the current understanding of O_3 effects at the ecosystem level especially long-term factorial experimental approaches are required that address questions of interactions of O_3 with other environmental factors more systematically. Such efforts should be underpinned by a more mechanistic research trying to better understand the various interactive feedbacks of the components of a particular system under O_3 exposure, e.g. by applying ecophysiological and molecular approaches.

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