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Review of the influence of climate change on the impacts of ozone on vegetation

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EXECUTIVE SUMMARY

Background and aims

Many studies have been conducted on the impacts of ozone (O_3) pollution on vegetation, ranging from effects at the cellular level to predicting impacts on a regional and international scale. However, it is becoming increasingly important when predicting future impacts of O_3 to consider O_3 effects within the context of global climate change. This review focuses on the interactive impacts of enhanced O_3 exposure and other climate change factors, in particular warming and atmospheric CO_2-enrichment, on terrestrial ecosystems. Whereas the emphasis is on the results from large scale ecosystems studies, comparisons with controlled environment chamber studies are included as often these studies are the only available source of data. This review primarily considers the impacts on crops and trees and focuses on above-ground vegetation responses. The review provides a cross-policy area document and the aims are:

- To assess the published literature on the influence of climate change on the response of vegetation to O_3;
- To summarise implications for policy makers.

The report contains a brief review of background information followed by consideration of O_3 flux and detoxification in a changing climate, impacts of climate change on the whole plant response to O_3 and consequences for pests and diseases, and policy implications.

Current European levels of tropospheric O_3 have been shown to cause damage to crops, trees and (semi-)natural vegetation. Effects-based research has resulted in the establishment of critical levels of O_3 for vegetation. Historically, critical levels of O_3 for vegetation were based on the concentration of O_3 in the atmosphere, but it has long been recognised that plant responses to O_3 are more closely related to the internal O_3 dose in the leaf modelled as the instantaneous flux of O_3 through the stomata, than the ambient O_3 concentration. Recently, stomatal flux-based critical levels for O_3 were defined for selected crop species and provisionally for trees. These take into account the varying influences of temperature, water vapour pressure deficit (VPD), light, soil water potential (SWP), atmospheric O_3 concentration and plant development (phenology) on O_3 uptake. Climate change factors such as elevated CO_2, temperature and precipitation will affect the flux of O_3 into leaves via direct or indirect impacts on stomatal conductance (g_s), VPD, SWP and phenology.

Impacts of global change on the flux of ozone

The overall impact of warming on the canopy flux of O_3 is difficult to predict and will depend on the location of the vegetation, severity and timing (e.g. summer or winter) of warming, its impacts on SWP and phenology of the vegetation. Each plant species has its own optimum temperature for g_s and the impact of warming on g_s will depend on which part of the temperature response function corresponds with the current ambient temperature. For example, in temperate, moist climates an increase in temperature is likely to result in an increase of the stomatal uptake of O_3, whereas in plants currently operating at their optimum temperature for g_s, warming is likely to result in a decrease of the stomatal uptake of O_3. The impacts of global warming on the canopy uptake of O_3 will also be affected by indirect effects, e.g. warming will result in an increase in VPD and decrease in SWP, which will generally result in a decrease in the stomatal flux of O_3 into leaves and warming will enhance plant development, which will reduce the stomatal flux of O_3 into leaves at a later stage of development. Little empirical data is available on the interactive impacts of O_3 and warming on vegetation, in particular at the field scale.

Many studies have shown that atmospheric CO_2-enrichment reduces g_s. Therefore, when plants were exposed to O_3 in the presence of elevated CO_2, the uptake of O_3 was often reduced. In general, elevated CO_2 ameliorates O_3-induced stress and the combined effects of O_3 and CO_2-enrichment on plant growth and physiology has often been near neutral as elevated CO_2 and O_3 affect vegetation in opposite ways. Effects of changes in precipitation patterns are likely to be mediated directly through (a) effects of VPD on g_s with increasing VPD causing a decrease in flux and (b) changes in SMD, with increasing SMD resulting in decreased stomatal flux and vice versa. The little data that is available on interactive impacts of elevated CO_2 and warming on vegetation indicate that the combined impacts of elevated CO_2 and temperature on vegetation might be complex.

Impacts of climate change on ozone detoxification within plants

In addition to the flux of O_3 into the stomata, subsequent detoxification of O_3 inside the leaves is a key determinant of the ultimate response of vegetation to O_3. Both the absolute level of antioxidants and the capacity to enhance antioxidant levels in response to O_3 might contribute to protect photosynthetic machinery and membrane functions from oxidative stress. Although CO_2-enrichment might primarily protect plants against O_3-induced damage by reducing the stomatal flux of O_3 (see above), additional detoxification of O_3 within the leaf cannot be excluded. However, a general ameliorating effect of CO_2-enrichment on O_3-induced oxidative stress via changes in the antioxidant status of leaves has not been proven as experimental data are inconclusive. Impacts of temperature on the antioxidant status of leaves have mainly been reported in relation to chilling or heat stress rather than the effects of a few degrees rise in temperature and thus cannot be used within a global warming context.

Ecosystem responses to combined ozone and climate change

Within ecosystems, vegetation responses to climate change are driven by complex interactions between abiotic and biotic factors such as atmospheric CO_2, temperature, nutrient and water availability, atmospheric pollutants, soil characteristics, land-use/management and species composition/diversity, and therefore are difficult to predict. Responses of plants to CO_2 enrichment, O_3 enrichment or warming are highly species-specific and the behaviour of species mixtures to these environmental changes can often not be predicted from responses by isolated plants. For example, in heterogeneous plant communities where the O_3 concentration decreases within the canopy with depth, species in the bottom layer of the canopy are exposed to lower O_3 concentrations and fluxes than species at the top of the canopy. Therefore, plant species identified as O_3-sensitive when grown as individual plants might not be so much affected by O_3 in a plant community if they grow in the bottom layer of the canopy. More knowledge is needed on the relationship between the responses of individual plant species and (semi-)natural plant communities to O_3 and climate change, because species competition is likely to influence the effects of O_3 and climate change on individual plant species. In addition, interactions between different species at various trophic levels are expected to change in a future climate. Because insect and plant species show individual responses to drivers of climate change, it is expected that climate change will affect the temporal and spatial association between species interacting at different trophic levels.

Due to high costs involved, data have emerged only in the last decade on the impacts of climate change on plant communities and ecosystems at the field scale under more natural conditions, i.e. without being confounded by artificial greenhouse-like conditions inside exposure chambers. As with exposure chambers, the majority of field studies have reported on the impacts of single drivers of climate change (such as elevated CO_2 or O_3 concentrations or warming) on plant communities and ecosystems, crops and trees in particular. Although Free Air Carbon dioxide/Concentration Enrichment (FACE) studies generally substantiate predictions based on chamber studies, some inconsistencies between the results of chamber and FACE studies have been reported. For example, grain crop yields increased far less than anticipated from prior enclosure studies and the responses of trees to elevated CO_2 might have been underestimated in chamber studies compared with FACE studies. Reported differences between the findings within FACE and prior chamber experiments show the need to aim for a wider use of FACE in both elevated CO_2 and elevated O_3 exposure studies and in particular with respect to (semi-)natural vegetation. However, large scale chamber studies are still required to further develop a mechanistic understanding of plant community responses to elevated O_3 and climate change, in particular for (semi-)natural vegetation.

In addition, vegetation responses to changes in single drivers of climate change cannot simply be scaled up to responses to changes in multiple drivers. There is a clear need for a combined approach of multifactorial experiments and modelling to improve predictions on the impacts of climate change on ecosystems in the long term. More field-scale experiments with (semi-) natural vegetation are needed to assess their long-term vulnerability to O_3 pollution and climate change. Elevated O_3 at relatively low concentrations can significantly reduce the growth enhancement by elevated CO_2 and therefore reduce C sequestration. This may mean that worldwide growth stimulations will not be as great as predicted from previous experimental and modelling studies with elevated CO_2. It is important to bring an understanding of O_3 as a moderator of climate change responses in global models of terrestrial net primary productivity and C sequestration.

Research recommendations

- The influence of climate change should be taken into account when predicting the future effects of O_3 on vegetation.

- In the first instance, the O_3-flux modelling procedures outlined in the Mapping Manual (LRTAP Convention, 2004) will need revising to include CO_2 concentration as a modifying factor.

- In the longer-term, it may be necessary to develop alternative modelling procedures since the current method is based on the stomatal responses to climatic and plant factors considered in isolation rather than in combination.

- There is a clear need for multi-factorial experiments to provide information for O_3-effect modelling. Because of the high cost involved with FACE systems, these may only be possible using enclosed or semi-enclosed chamber systems especially where warming and CO_2 are considered as factors.

- As very little is known about the vulnerability of communities of (semi-)natural vegetation to O_3 and climate change, there is an urgent need for experiments that enhance our understanding of the impacts on vegetation responses and species competition. With little information available, much progress could be made in the short-term by conducting experiments with closed or semi-enclosed exposure systems. Despite the higher costs and increased complexity, the longer-term aim should be to conduct FACE experiments to assess the vulnerability of (semi-)natural vegetation to O_3 and climate change.

- There is a need for a wider and longer-term use of FACE for crops and forest trees to expand the range of species for which data exists and to determine the cumulative effects over several years.

- So far, FACE experiments have focussed on temperate ecosystems, while tropical, boreal and arctic systems have been largely ignored. FACE experiments with tropical forests, representing 50% of C in terrestrial biomass, are an obvious international need.

CONTENTS

1. Introduction

Many studies have been conducted on the impacts of ozone (O_3) on vegetation, ranging from effects at the cellular level to predicting impacts on a regional and international scale. Predictions have tended to be for 2010, and sometimes 2020, and although complex modelling methods have been used, they are based on O_3 effects studied in isolation. However, it is becoming increasingly important when predicting future impacts of O_3 to consider O_3 effects within the context of global climate change. This review focuses on the interactive impacts of enhanced O_3 exposure and other climate change factors, in particular warming and atmospheric CO_2-enrichment, on terrestrial ecosystems. Whereas the emphasis is on the results from large scale ecosystems studies, comparisons with controlled environment chamber studies are included as often these studies are the only available source of data. At the field scale we are not aware of studies investigating the interactive impact of O_3 exposure and climate change on (semi-)natural vegetation, hence, this review primarily considers the impacts on crops and trees. This study focuses on above-ground vegetation responses, consequences for biodiversity and carbon sequestration are only briefly mentioned. The review provides a cross-policy area document that will be presented to the Working Group on Effects of the Convention on Long-range Transboundary Air Pollution as a deliverable from the ICP Vegetation.

The aims of this review are:

- To assess the published literature on the influence of climate change on the response of vegetation to O_3;
- To summarise implications for policy makers.

The report contains a brief review of background information followed by consideration of O_3 flux and detoxification in a changing climate, impacts of climate change on whole plant response to O_3, interacting influences of O_3 on pests and diseases, and policy implications.

2. State of knowledge of climate change and its impacts on vegetation

2.1 Predicted changes in the climate in the 21st century

The global climate has changed dramatically since the onset of the industrial revolution. Trace gases such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and ozone (O_3) are continuing to increase in the atmosphere. These and other greenhouse gases such as halocarbons trap the outgoing radiation from the surface of the earth to heat the atmosphere. Recently, the Intergovernmental Panel on Climate Change (IPCC) concluded that a change in global mean temperature of 1.4-5.8 ^{o}C, in combination with changes in precipitation patterns and an increased frequency of extreme weather events, is likely to occur in the 21st century (IPCC, 2001a). Depending on emissions scenarios, the following changes are predicted for trace gases by the end of the 21st century (IPCC, 2001a):

- Increase in CO_2 concentration to 540-970 ppm;
- Change in CH_4 concentration between -190 to +1,970 ppb;
- Increase in N_2O concentration between 38-144 ppb;
- Change in O_3 concentration between -12 to +62%.

The high spatial and temporal variability in O_3 concentrations mean that it is difficult to identify with great confidence any long-term trends and make predictions for the future. However, there is evidence that the mean ground-level O_3 concentrations over the UK and in the rest of Europe are increasing and the peak concentrations are declining (NEGTAP, 2001). In the future, peak concentrations of O_3 will probably be reduced further with the implementation of the Gothenburg Protocol (Working Group on Effects, 2004), but this should be considered in the context of an increasing global background concentration. In the UK, the annual average O_3 concentration varies considerably across the landscape from low values around 10 ppb in urban/industrial regions to 25 ppb in the countryside and 35 ppb in upland areas (NEGTAP, 2001).

Based on recent global model simulations it is very likely that nearly all land areas will warm more rapidly than the global average, particularly those at northern high latitudes in the cold season. Most notable of these is the warming in the northern regions of North America, and northern and central Asia, which exceeds global mean warming in each model by more than 40%. In contrast, the warming is predicted to be less than the global mean change in south and south-east Asia in summer and in southern South America in winter (IPCC, 2001a). For a wide range of scenarios, global model simulations predict an increase in global average water vapour concentration and precipitation during the 21st century. By the second half of the 21st century, it is likely that precipitation will have increased over northern mid to high latitudes and Antarctica in winter. At low latitudes there are both regional increases and decreases over land areas. Larger year to year variations in precipitation are very likely over most areas where an increase in mean precipitation is projected (IPCC, 2001a).

Regarding extreme weather events, the following changes are predicted to occur during the 21st century (IPCC, 2001a):

- Higher maximum temperature and more hot days over nearly all land areas;
- Higher minimum temperature and fewer cold and frost days over nearly all land areas;
- Reduced diurnal temperature range over nearly all land areas;
- Increase in heat index over land areas;
- More intense precipitation events;
- Increased summer continental drying and associated risk of drought;
- Increase in tropical cyclone peak wind intensities;
- Increase in tropical cyclone mean and peak precipitation intensities.

More specifically, the following climate changes are predicted for the UK with 2080 as the reference year (Hulme *et al*., 2002):

- Annual average temperature may rise between 2 and 3.5 ^{o}C. There will be greater warming in the south and east than in the north and west, and there may be greater warming in the summer and autumn than in winter and spring;
- High summer temperatures will become more frequent and very cold winters will become increasingly rare;
- Winters will become wetter and summer may become drier everywhere;
- Snowfall amounts will decrease throughout the UK;
- Heavy winter precipitation (rain and snow) will become more frequent.

2.2 Impacts of climate change on vegetation

Changes in climate will affect terrestrial ecosystems at different temporal and spatial scales, ranging from effects at the global biosphere levels which may take years to millennia, to localized effects at the level of individual organisms, which may take only minutes to a few years (IPCC, 2001b). Terrestrial ecosystems are subject to many pressures, such as land-use changes (including habitat fragmentation), climate change, deposition of pollutants and nutrients, harvesting, grazing by livestock, introduction of exotic species and natural climate variability. The impact of climate change on these systems will be influenced by land and water management adaptation and interactions with other pressures. In general, adaptive capacity is greater for more intensively managed lands in production of market goods (e.g. intensively managed agricultural ecosystems, timber production in plantations) than in less intensively managed lands and non-market values of those lands (IPCC, 2001b; Fuhrer, 2003). Species composition and dominance will change, but these changes are likely to lag behind the changes in climate by years to decades to centuries (IPCC, 2001b).

Within ecosystems, vegetation responses to climate change are driven by complex interactions between abiotic and biotic factors such as atmospheric CO_2, temperature, nutrient and water availability, atmospheric pollutants, soil characteristics, land-use/management and species composition/diversity, and therefore are difficult to predict (e.g. Shaw *et al*., 2002; Beier, 2004; Harmens *et al*., 2004). Responses of plants to CO_2 enrichment or warming are highly species-specific and the behaviour of species mixtures to these environmental changes can often not be predicted from responses by isolated plants (see Fuhrer *et al*., 2003 and Harmens *et al*., 2004). In addition, interactions between different species at various trophic levels are expected to change in a future climate as insect and plant species show individual responses to drivers of climate change. Climate warming also disturbs the synchrony between temperature and photoperiod (see Fuhrer, 2003), because insect and host plant species show individualistic responses to temperature and photoperiod. Therefore, it is expected that climate changes will affect the temporal and spatial association between species interacting at different trophic levels (Harrington *et al*., 1999).

Several studies have indicated that the impacts of elevated CO_2 and temperature on vegetation are complex (Shaw *et al*., 2002; Fuhrer, 2003; Norby and Luo, 2004). Direct effects of elevated atmospheric CO_2 concentration on crop yield suggests that beneficial effects may be greater under certain stressful conditions, including warmer temperature and drought (IPCC, 2001b) There is ample evidence that warming reduces the yield of grain crops because of accelerated plant development (see Amthor, 2001) and the negative effect tends to be larger for grain yield than for total biomass (e.g. Batts *et al*., 1997). This may be due to the particular temperature sensitivity of grain fill. Warming by only a few degrees may offset the positive effect of elevated CO_2 on yield in wheat (Amthor, 2001) and in herbaceaous species (Porter and Perez-Soba, 2001). Conversely, elevated CO_2 might counteract the negative effect of higher temperature in cool-temperate grasses (Nijs *et al*., 1996). Exposure of a (semi-)natural grassland for four years to elevated CO_2 and temperature hardly showed any significant interactions between CO_2 and temperature. On the other hand, significant interactions with grassland management were observed (Harmens *et al*., unpublished). However, in a field-scale experiment using annual grassland, the positive effect of warming on net primary productivity was dampened by elevated CO_2 (Shaw *et al*., 2002).

2.3 Impacts of ozone on vegetation

Current European levels of tropospheric O_3 have been shown to cause damage to agricultural crops, forests trees and (semi-)natural vegetation (Kärenlampi and Skärby, 1996; Fuhrer and Achermann, 1999; Karllson *et al*., 2003). Many crop species such as wheat, soybean and tomato are sensitive to the pollutant (Table 1), with reductions in the quantity and quality of the yield being reported at the concentrations experienced within Europe (Mills *et al*., 2003). Effects-based research has resulted in the establishment of critical levels for O_3. Historically, critical levels of O_3 for vegetation were based on the concentration of O_3 in the atmosphere, but it has long been recognised that plant responses to O_3 are more closely related to the internal O_3 dose in the leaf, or the instantaneous flux of O_3 through the stomata, than the ambient O_3 exposure (e.g. Fuhrer *et al*., 1992). Avoidance by stomatal closure, detoxification of free radicals through endogenous scavenging systems, and induction of defence genes might explain differential O_3 tolerance among plant species (Lee, 2000). Stomatal closure would be the first opportunity for the plant to resist the onset of O_3 damage.

The negative effect of O_3 on the crop yield of many species is due to a limitation of photosynthetic C assimilation resulting from a reduction in the activity and amount of Rubisco (Farage and Long, 1992; Pell *et al*., 1994; Lehnherr *et al*., 1997), associated with accelerated leaf senescence (Grandjean and Fuhrer, 1989). In addition, O_3 results in an impaired translocation of photosynthate from source to sinks (Grantz and Farrar, 1999; Grantz and Yang, 2000; Sild *et al*., 2002). In wheat most of the O_3-induced changes in carbohydrate concentrations were associated with accelerated leaf and plant senescence (Sild *et al*., 2002). O_3 also affects the quality of crops; for instance, grain N concentration in wheat increases with increasing O_3 (Pleijel *et al*., 1999), leading to a better baking quality of the flower (Fuhrer *et al*., 1990), whereas in potato increasing O_3 had a negative impact on tuber quality (Vorne *et al*., 2002). In grapevines the juice quality of grapes was more sensitive to O_3 than the yield (Soja *et al*., 2004). In oilseed rape seed quality was reduced by elevated O_3 in terms of crude protein and oil content (Ollerenshaw *et al*., 1999).

Table 1 The range of sensitivity of agricultural and horticultural crops to ozone (see Mills *et al*., 2003 for response functions and definition of sensitivities).

Sensitive	Moderately sensitive	Moderately resistant	Insensitive
Cotton, Lettuce, Pulses, Soybean, Salad Onion, Tomato, Turnip, Watermelon, Wheat	Potato, Rapeseed, Sugarbeet, Tobacco	Broccoli, Grape, Maize, Rice	Barley, Fruit (plum & strawberry)

In the most recent revision of the Mapping Manual (LRTAP Convention, 2004), stomatal flux-based critical levels for O_3 were defined for selected crop species (wheat and potato) and provisionally for trees (beech and birch) in addition to concentration-based critical levels. The flux-based approach required the development of mathematical models to estimate stomatal flux, primarily from knowledge of stomatal responses to environmental factors. Stomatal flux-based critical levels for O_3 take into account the varying influences of temperature, water vapour pressure deficit (VPD), light, soil water potential (SWP), atmospheric O_3 concentration and plant development (phenology) on O_3 uptake (Emberson *et al*., 2000; LRTAP Convention, 2004). For example, for a given O_3 concentration the stomatal flux of O_3 in warm, humid conditions with moist soil is greater than that in hot, dry conditions with dry soil because the stomata will be more open. Flux-based critical levels therefore provide an estimate of the critical amount of O_3 entering through the stomata and reaching the sites of action inside the plant. Climate change factors such as elevated CO_2, temperature and precipitation will affect the flux of O_3 into leaves via direct or indirect impacts on stomatal conductance (g_s), VPD, SWP and plant development.

The flux models developed so far are based on the responses of sun-lit leaves at the top of a uniform crop or tree canopy as these contribute most to the uptake of O_3 by the whole canopy (Emberson *et al*., 2000; Hayes, pers. comm.). Efforts are currently focussed on establishing canopy flux-response relationships that take into account different stomatal fluxes in shaded rather than sun-lit leaves, the penetration of irradiance into the canopy estimated using a canopy extinction algorithm, O_3 concentration gradients within the canopy, leaf area index and leaf age effects within the full canopy (Mills *et al*., 2005). Such differences are particularly important in heterogeneous plant communities such as unmanaged grasslands and heaths where the O_3 concentration decreases within the canopy with depth (Davison *et al*., 2003) and species in the bottom layer of the canopy are exposed to lower O_3 concentrations and fluxes than species at the top of the canopy. Therefore, plant species identified as O_3-sensitive when grown as individual plants might not be so much affected by O_3 in a plant community if they grow in the bottom layer of the canopy. On the other hand, low light intensity in the canopy may increase the sensitivity of plants to O_3 (see Fuhrer *et al*., 2003).

2.4 Experimental approaches for studying ozone and climate change interactions

Thousands of studies have reported on the impacts of single drivers of climate change (such as elevated CO_2 or O_3 concentrations or warming) on individual plant species in more or less controlled environment chambers, including greenhouses. Only in the last decade, have data emerged on the impacts of climate change on plant communities and ecosystems at the field scale. Such studies have used expensive Free Air Carbon dioxide/Concentration Enrichment (FACE) systems for the gases CO_2 and O_3 (Kimball *et al.*, 2002; Nowak *et al.*, 2004; Ainsworth and Long, 2005) and have applied systems to warm ecosystems at the field scale (Rustad *et al.*, 2001; Shaw *et al.*, 2002; Peñuelas *et al.*, 2004). These systems allow effects on ecosystems to be studied under more natural conditions without being confounded by artificial greenhouse-like conditions inside exposure chambers (Hendrey *et al.*, 1993; McLeod and Long, 1999). For example, enclosure inside exposure chambers has been shown to amplify down-regulation of photosynthesis and production (Morgan *et al.*, 2001), and may through environmental modification produce a chamber effect that exceeds the effect of CO_2-enrichment. Even semi-open systems such as open-top chambers, have been shown to overestimate CO_2 effects on plants (Van Oijen *et al.*, 1999).

The following inconsistencies between the results of chamber and FACE studies have been reported:

- In the open field, elevated CO_2 appears to reduce crop g_s about one and a half times more than observed in previous chamber experiments (Kimball *et al.*, 2002);
- In crops elevated CO_2 appears to have stimulated root growth relatively more than shoot growth under FACE compared to chamber conditions (Kimball *et al.*, 2002);
- Grain crop yields increased far less than anticipated from prior enclosure studies (Ainsworth and Long, 2005);
- FACE studies showed that grasslands had greater productivity enhancement in drier years, in agreement with predictions based on chamber studies, however, this was not true for forests (Nowak *et al.*, 2004);
- Forests have significantly greater enhancement than grasslands (Nowak *et al.*, 2004) and trees were more responsive than herbaceous species to elevated CO_2 (Ainsworth and Long, 2005). Results for plant functional type do not generally fit earlier predictions that certain groups of plants such as legumes and C_3 plants will have greater enhancement of productivity than woody and C_4 plants (Nowak *et al.*, 2004);
- The reduction in plant nitrogen was small and largely accounted for by a decrease in Rubisco (Ainsworth and Long, 2005). However, most herbaceous species had reduced leaf nitrogen content under elevated CO_2, whereas most woody species had little change in leaf N (Nowak *et al.*, 2004).

Despite these differences, recent reviews of results from FACE studies generally substantiate previous predictions based on chamber studies, such as an increase in light-saturated carbon uptake, diurnal C assimilation, growth and above-ground production and a decrease in specific leaf area and g_s at elevated CO_2 (Ainsworth and Long, 2005). Overall, the leaf area index was not affected significantly by CO_2-enrichment, but differences between functional groups were present, such that herbaceous C_3 grasses did not show significant changes in leaf area index, whereas the leaf area index was enhanced by 21% in trees (Ainsworth and Long, 2005).

Open-air exposure in SoyFACE suggest that the effects of elevated O_3 on an O_3-sensitive plant such as soybean are substantially less than those predicted by prior chamber studies, particularly during vegetative growth (Morgan *et al*., 2004). This might be related to a lower accumulated exposure to O_3 during the life cycle of vegetative leaves as these are continuously overlain by new layers of leaves and are shaded lower in the canopy. As the O_3 concentration declines with canopy depth, these leaves will be exposed to lower O_3 concentrations during the later stage of development, whereas in chamber studies they might be exposed to higher O_3 concentrations throughout their life cycle due to stirring of the air in chambers.

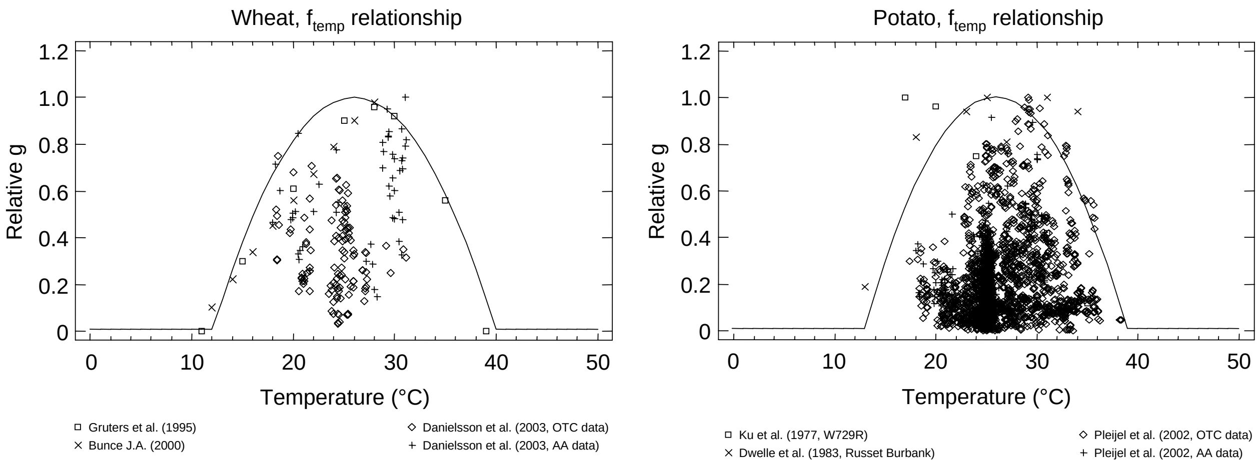
3. Impacts of climate change on the stomatal flux and detoxification of ozone

The flux of O_3 into the stomata and its subsequent detoxification are key determinants of the ultimate response of the plant to the pollutant. Since both are highly dependant on climatic conditions, there is significant potential for the predicted changes in the climate to influence the response to O_3 through an effect on rates of flux and detoxification. Effects can be direct – e.g. temperature, CO_2 and humidity effects on g_s or indirect via an influence on soil water potential (SWP) and plant development.

3.1 Impacts of warming on the stomatal flux of ozone

The stomatal response to leaf temperature is described by a parabolic function (Emberson *et al.*, 2000) with a minimum temperature at which stomatal opening occurs and an optimum temperature for g_s (Figure 1). Each plant species will have its own optimum temperature for g_s and the impact of climate warming on g_s will depend on which part of the temperature response function corresponds with the current ambient temperature. In temperate, moist climates an increase in temperature is likely to result in an increase of g_s and therefore an increase in the stomatal uptake of O_3, possibly resulting in enhancement of leaf damage caused by O_3. For those plants already at their optimum temperature for g_s, warming is likely to result in a decrease of g_s and stomatal uptake of O_3, possibly resulting in a reduction of leaf damage by O_3. The changes described can be predicted for sunlit leaves at the top of the canopy, however, the consequences for the stomatal flux into the whole canopy are as yet unknown. Consideration of the effect of warming on flux in combination with associated changes in precipitation and CO_2 concentration is provided in Section 3.4.

Figure 1. Parameterisation of wheat and potato stomatal conductance models. The function shown (f_{temp}) describes the dependence of the relative stomatal conductance (g) on temperature (see chapter 3 of the Mapping Manual (LRTAP Convention, 2004) for details).



3.2 Impacts of increased CO_2 concentration on the stomatal flux of ozone

Many short- and long-term studies have shown that plants grown in an elevated CO_2 environment have reduced g_s (e.g. Drake *et al.*, 1997; Curtis and Wang, 1998; Medlyn *et al.*, 2001). An extensive analysis of field-grown forest species to longer-term (>1 year) CO_2-enrichment showed an average reduction in g_s of 21% with no evidence of stomatal acclimation (Medlyn *et al.*, 2001). As expected, exposing plants to O_3 in the presence of elevated CO_2 therefore reduced the uptake of O_3 (Fiscus *et al.*, 1997; McKee *et al*, 1997; Kollist *et al.*, 2000). In potato this CO_2-induced reduction in g_s was not affected by exposure to O_3 *per se* (Vandermeiren *et al.*, 2002), and thus when considered in isolation, increasing CO_2 concentrations are likely to decrease O_3 uptake. An in-depth review of the mechanisms of tree stomatal responses to elevated CO_2 and O_3 was conducted recently by Paoletti and Grulke (2005).

3.3 Impacts of changes in precipitation patterns on the stomatal flux of ozone

In simplest terms, effects of changes in precipitation patterns are likely to be mediated directly through (i) effects of VPD on g_s with increasing VPD causing a decrease in flux and (ii) changes in SMD, with increasing SMD resulting in decreased stomatal flux and vice versa (Figure 2). Interactions between O_3 stress and plant water use efficiency (WUE) are important due to the co-occurrence of high O_3 levels, combined with reduced soil moisture during warming. A reduction in soil moisture below a threshold will reduce the stomatal flux of O_3 (Figure 2), resulting in less O_3 uptake and damage in plants during peak levels of O_3.

3.4 Effects of combined changes on ozone flux

The summarised information presented in Sections 3.1 to 3.3 assumes that the predicted changes are occurring in isolation. However, the situation is far more complex than this as the various changes associated with climate change will act together to influence stomatal uptake. Unfortunately, it is not currently possible to give an overview of the predicted effects of the combined effects of all factors on the flux of O_3. Some examples are provided to illustrate the complexity of the interactions:

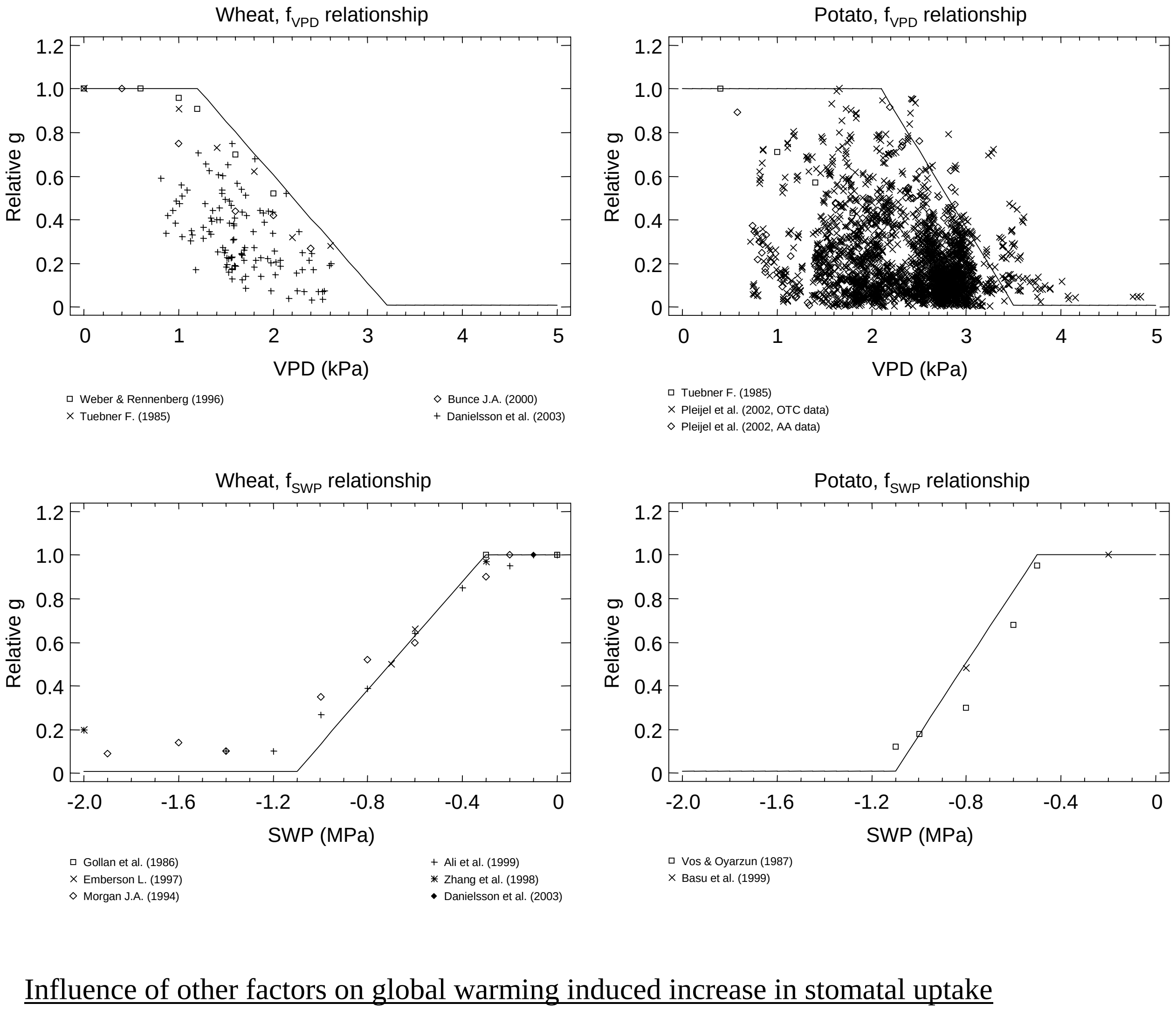
Elevated CO_2 increases leaf temperature

Whilst a rise in CO_2 levels would be expected to reduce stomatal opening and thus reduce uptake, the reduced g_s will increase leaf temperature due to a reduction in cooling of the leaves by evapotranspiration, which adds to an enhanced affect of temperature on g_s. In FACE systems rises in canopy temperatures between 0.6 and 1.1 ^{o}C have been reported at elevated CO_2 concentrations and such increases should be added to those predicted for global warming (Kimball *et al.*, 2002). The resultant increase in leaf temperature would either increase or decrease conductance depending on whether the optimum temperature for g_s has been reached. Potentially, the effects of elevated CO_2 and temperature on the g_s of leaves could cancel each other out.

Responses to soil moisture changes at elevated CO_2

In general, decreases in g_s with elevated CO_2 are exacerbated by drought stress which also tends to close stomata (Kang *et al.*, 2002; see Ainsworth and Long, 2005). Partial closure of stomata results in increased water use efficiency (WUE) for plants indicating that plants may be more able to withstand moderate water stress. However, improved WUE detected at the leaf level may not cause the expected reduction in whole plant water consumption as whole canopies may still consume equal amounts or even more water due to an elevated CO_2-induced increase in total leaf area and leaf temperature (Riedo *et al*., 1999; Hui *et al*., 2001; Kimball *et al*., 2002). Elevated CO_2 tends to increase soil moisture by reducing plant water uptake (Owensby *et al*., 1999; Kimball *et al*., 2002), which could potentially result in a lower reduction in g_s and uptake of O_3. However, for trees, changes in volumetric soil moisture were only detectable during relatively dry years but not in relatively wet years (Karnosky *et al*., 2003). In general, elevated CO_2 will reduce the leaf uptake of O_3, but the impact of CO_2 enrichment on O_3 uptake at the canopy level will also be affected by elevated CO_2-induced changes in leaf area index and soil moisture.

Figure 2. Parameterisation of wheat and potato stomatal conductance models. The functions shown (f_{VPD} and f_{SWP}) describe the dependence of the relative stomatal conductance (g) on vapour pressure deficit (VPD) and soil water potential (SWP) (see chapter 3 of the Mapping Manual (LRTAP Convention, 2004) for details).



<u>Influence of other factors on global warming induced increase in stomatal uptake</u>

The complexity of the interactions between the factors involved in climate change is well illustrated by consideration of the impacts of global warming on the canopy uptake of O_3. When considered as a single factor, increased temperature is likely to increase stomatal uptake of O_3 providing the optimum for gs has not been reached (Section 3.1). However, the response to warming will also be affected by the following indirect effects:

- Providing the precursors are present, an increase in warming would increase the rate of tropospheric O_3 formation with consequent increase in O_3 concentration surrounding the leaves and available for stomatal uptake;
- Warming will result in a increase in VPD and decrease in SWP (soils will dry out faster due to enhanced soil evaporation and enhanced canopy evapotranspiration), which will generally result in a decrease in the stomatal flux of O_3 into leaves due to a reduction in g_s (Emberson *et al*., 2000). (Semi-) arid regions are likely to be most sensitive to warming as the potential evapotranspiration increases by about 2-3% for each 1 ^oC rise in temperature (see Fuhrer, 2003);
- Warming will enhance plant development, which will reduce the stomatal flux of O_3 into leaves at a later stage of development (Emberson *et al*., 2000).

Thus, the overall impact of warming on the canopy flux of O_3 is difficult to predict and will depend on the severity and timing (e.g. summer or winter) of warming, the current SWP and the phenological stage of the vegetation. However, it seems likely that global warming when considered in isolation, will increase O_3 uptake in temperate climates.

3.5 Detoxification of ozone in plants in a changing climate

Both the absolute level of antioxidants and the capacity to enhance antioxidant levels in response to O_3 might contribute to protect photosynthetic machinery and membrane functions from oxidative stress. However, in contrast with the general reduction of uptake of O_3 by plants due to a reduction in g_s at elevated compared with ambient CO_2, impacts of CO_2-enrichment on the antioxidant status of leaves are not consistently reported within the literature. In barley, primary leaves developed early senescence at elevated compared with ambient CO_2, which was associated with a decline in antioxidant capacity, resulting in oxidative stress (Robinson and Sicher, 2004). These results suggest that protection of aging leaves from O_3 damage might be reduced at elevated compared with ambient CO_2. In contrast, Rao *et al*., (1995) indicated that elevated CO_2 might protect wheat leaves against O_3-induced oxidative stress by prolonged enhancement of the antioxidant status. Mc Kee *et al*. (1997) concluded that stomatal exclusion rather than the antioxidant status plays a major role in the protective effect of elevated CO_2 against O_3 damage in wheat.

Leaves of *Dactylis glomerata* L. and *Trifolium repens* L. showed no difference in antioxidant status (regarding protein content, activity of oxidant-scavenging enzymes and lipid peroxidation) when exposed to elevated CO_2 in mini-FACE rings in a semi-natural grassland community. The effects of elevated CO_2 on the leaves of plants within the semi-natural grassland community were extremely variable, species-specific and rather limited (di Toppi *et al*., 2002). Contrasting results have also been reported for sugar maple: CO_2-enrichment might protect to some extent against O_3 damage by providing additional carbon and energy through increased net assimilation (Gaucher *et al*., 2003), but Niewiadomska *et al*. (1999) concluded that elevated CO_2 does not provide enhanced tolerance to oxidative stress. Although elevated CO_2 stimulated iron superoxide dismutase activity in chloroplasts, this did not result in enhanced protection against the detrimental effects of O_3, most probably due to compartmentation of CO_2 and O_3 effects within the cell (Niewiadomska *et al*., 1999). In oak trees permanently exposed to elevated CO_2 within the vicinity of natural CO_2 springs, the activities of antioxidant enzymes tended to be lower and the ascorbate pool tended to be larger and more in reduced form, suggesting an attenuation of the oxidative risk in CO_2-enriched oak trees (Marabottini *et al*., 2001). In aspen clones varying in O_3 sensitivity elevated CO_2 did not ameliorate the harmful effects of O_3, in contrast, it may have contributed to an increase in chloroplast damage in all clones (Wustman *et al*., 2001).

In summary, a general ameliorating effect of CO_2-enrichment on O_3-induced oxidative stress via changes in the antioxidant status of leaves has not been proven as experimental data are inconclusive. Predictions cannot yet be made for impacts of small increases in temperature on the antioxidant status of leaves, since temperature effects have mainly been reported in relation to chilling or heat stress rather than the effects of a few degrees rise in temperature.

4. Impacts of ozone on growth and yield in a changing climate

As stated earlier many studies have examined the impact of O_3 and climate change on vegetation in isolation rather than in combination. In this chapter the impacts of O_3 on plant growth, productivity and quality will be described briefly, followed by any known interactions with climate change. As little is known about the combined impacts of O_3 and climate change on (semi-)natural vegetation, primarily the impacts on crops (section 4.1) and trees (section 4.2) will be reviewed.

4.1 Crops

Yield and quality

In general, elevated CO_2 reduces O_3-induced leaf damage and yield losses, primarily through O_3 exclusion via a reduction in g_s rather than increased detoxification capacity (see Section 2.3 and Fuhrer, 2003). However, the extent of such protection provided by CO_2-enrichment varies and can depend upon the degree of stomatal closure induced by elevated CO_2, which differs between taxa, and/or upon the timing and duration of O_3 exposure (see Craigon *et al.*, 2002). The relative yield stimulation by elevated CO_2 tends to be larger in an atmosphere with elevated levels of O_3, or vice versa, in a CO_2-enriched atmosphere, negative effects of O_3 are less than at ambient CO_2. This was observed in soybean (Heagle *et al.*, 1998), cotton (Heagle *et al.*, 1999) and winter wheat (Heagle *et al.*, 2000), but not in clover (Heagle *et al.*, 1993). In potato, significant interactions between O_3 and CO_2 were observed regarding the glucose and reducing sugar content in tubers (Vorne *et al.*, 2002). In wheat, the grain yield was negatively affected by O_3 at ambient CO_2 but unaffected by O_3 at elevated CO_2 (Pleijel *et al.*, 2000). However, responses of wheat to elevated O_3 and CO_2 appear to be cultivar-dependant as some cultivars do not respond significantly to elevated O_3 levels and for those cultivars no significant interactions between O_3 and CO_2 were observed (Bender *et al.*, 1999). Despite the beneficial impact of CO_2 enrichment on growth and yield of C_3 cereal crops, declines in flour quality due to reduced N content are likely in a CO_2-enriched world (Fangmeier *et al.*, 1999), therefore counteracting the positive effect of O_3 on flour quality (Pleijel *et al.*, 1999).

Climate factors such as mean air temperature and global radiation might be more important factors affecting grain yield and biomass, although a large proportion of the observed variability sometimes remains unexplained (Bender *et al.*, 1999). As crops differ in O_3-sensitivity (LRTAP Convention, 2004), this will affect the species-specific responsiveness to climate change, which should be taken into account in future climate modelling. Stimulation of photosynthesis by CO_2 does not automatically translate into increased biomass or yield. In determinate crops such as cereals, grain yield not only depends on photosynthesis but also on the length of the active phase of leaf photosynthesis, and the sink capacity of the grains. In barley (*Hordeum vulgare* L.) elevated CO_2 increased the N sink capacity of the grains in combination with accelerated flag leaf senescence, which in turn, reduced the length of the period of photosynthetic C acquisition (Fangmeier *et al.*, 2000).

Often, the effects of CO_2 and/or O_3 have been studied with non-limiting supply of water and nutrients, and temperatures have been kept near the optimum for crop growth. Under these experimental conditions, average yield stimulation for C_3 crops with a doubling of CO_2 has been estimated at 30%, whilst estimates based on results from field-scale experiments under more realistic conditions including varying water availability were lower. According to a review by Kimball *et al*. (2002) of responses of agricultural crops to FACE, elevated CO_2 stimulates biomass in C_3 grasses by an average of 12%, grain yield in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) by 10-15%, and tuber yield in potato (*Solanum tuberosum* L.) by 28%. Yield stimulation in C_4 crops is much lower. However, exposure of the C_4 crop *Zea mays* (maize or corn) in a FACE study suggests that under field conditions it might be more responsive to elevated CO_2 than currently is predicted based on chamber studies, as leaf photosynthesis was significantly increased at elevated CO_2 (Leakey *et al*., 2004). Under limiting N supply in FACE experiments, a mean stimulation of wheat grain yield by only 7% was observed, in contrast to a higher relative stimulation under water-limited conditions (Kimball *et al*., 2002).

Nitrogen and water use efficiency

An increase in nitrogen use efficiency (NUE) has often been observed in response to CO_2-enrichment (Drake *et al*., 1997), resulting in a decrease in N yield in cereals (Kimball *et al*., 2002), because of a decrease in plant N concentration. Correspondingly, grain quality was reduced by CO_2 enrichment. For wheat, contrasting results for the impacts of O_3 stress on NUE have been reported (Fangmeier, 1999; Fuhrer, 2003). The combined effect of O_3 and CO_2 on NUE remains unknown.

Changes in the water balance and the amount of water available in the soil can be crucial for crop yield. In grasslands, 90% of the variance in primary production can be accounted for by the annual precipitation (see Campbell *et al*., 1997) and yield of water-limited crops is determined by crop water use and water use efficiency (WUE). Interactions between O_3 stress and WUE are important due to the co-occurrence of high O_3 levels, combined with reduced soil moisture during warm weather. Reduced leaf WUE in response to O_3 was found in wheat (Saurer *et al*., 1991) and soybean (Vozzo *et al*., 1995). This effect may be linked to direct negative effects of O_3 on stomatal functioning (Leipner *et al*., 2001; McAinsh *et al*., 2002) or the stronger sensitivity of photosynthetic CO_2 fixation relative to the g_s of water vapour (Saurer *et al*., 1991). But because of a concurrent reduction in crop biomass, O_3 is not likely having an effect on total crop water consumption.

While leaf-level responses to elevated CO_2 and O_3 are well documented, few studies have addressed canopy level responses to increases in these pollutants. In SoyFACE the results show a decrease in evapotranspiration for all three treatments with the largest decrease observed for growth in elevated O_3 (Bernacchi *et al*., unpublished). When integrated over the season, plants grown in elevated CO_2 and elevated O_3 used 10 and 18% less water, respectively. While the directional response of soybean exposed to increases in CO_2 and in O_3 were similar, the mechanisms for these responses differ. Growth in elevated O_3 resulted in a decrease in leaf area compared with the control. It is likely that the O_3-induced damage to the plant canopy, responsible for the lower biomass and leaf area, is responsible for the lower evapotranspiration in soybean. On the other hand, soybean grown in elevated CO_2 demonstrated higher leaf area while showing a reduction in evapotranspiration. These results suggest that a decrease in g_s was sufficient to more than offset the increase in leaf area associated with growth in elevated CO_2. These results imply that future atmospheric change may influence soybean response to drought conditions and may have feedback effects on atmospheric moisture, potentially altering regional precipitation patterns.

4.2 Trees

As for crops, elevated CO_2 and O_3 often affect trees in opposite ways (see Karnosky *et al.*, 2003). O_3 is generally detrimental to tree growth and forest productivity and induces foliar injury, decreases foliar chlorophyll concentrations, accelerates leaf senescence, decreases photosynthesis, alters carbon allocation and epicuticular wax composition, predisposes trees to attack by pests and decreases growth. In contrast to O_3, elevated CO_2 stimulates photosynthesis (Tjoelker *et al.*, 1998; Noormets *et al.*, 2001a,b) and growth above ground (Norby *et al.*, 1999) and below ground (King *et al.*, 2001; Kubiske and Godbold, 2001), and delays foliar senescence in the autumn (see Karnosky *et al.*, 2003).

Growth and photosynthesis

Karnosky *et al.* (2003) reviewed the results from the Aspen FACE project, in which the interactive impacts of CO_2 and O_3 were studied in a northern temperate forest containing two different functional groups: the indeterminate, pioneer, O_3-sensitive species trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) and the determinate, late successional, O_3-tolerant species sugar maple (*Acer saccharum*). The responses of these interacting greenhouse gases were remarkably consistent in pure aspen stands and mixed aspen/birch and aspen/maple stands, from molecular to ecosystem level, for O_3-tolerant as well as O_3-sensitive genotypes and across various trophic levels. After 3 years of exposure, CO_2-enrichment stimulated the above-ground volume of aspen stands by 40%. Unlike in other FACE studies (loblolly pine (Oren *et al.*, 2001) and sweetgum (Norby *et al.*, 2001)), there was no indication of a diminishing growth trend with time. In the Aspen FACE study, O_3 completely offset the growth enhancement by CO_2, both for O_3-sensitive and tolerant clones. The results are consistent from leaf to ecosystem level and across trophic levels in that elevated CO_2 and O_3 exerted opposite effects.

The detailed results from the Aspen FACE study revealed that there were species-specific and genotype-specific photosynthetic responses to CO_2, O_3 and CO_2+O_3. Elevated CO_2 increased upper canopy light-saturated CO_2 assimilation rate (A_{max}) in aspen and birch, but not in sugar maple. Net gain in daily canopy C fixation were largely realized at the top of the canopy and were driven by increases in A_{max}. However, increases in A_{max} due to elevated CO_2 were eliminated by elevated O_3. Leaf area index responses were similar to responses of A_{max} to treatments. Generally, the stomata of maple were more responsive than aspen and birch to changing environmental conditions (light, CO_2 and relative humidity) across all treatments. Elevated CO_2 tended to reduce g_s and the largest decreases in g_s for maple were under the combined CO_2 + O_3 treatment. Enhanced rates of photosynthesis under elevated CO_2 contributed to increased above-ground growth of aspen and birch. In contrast, decreases in photosynthesis by O_3 depressed above-ground growth in aspen, but not in birch. Interacting CO_2 and O_3 resulted in intermediate responses for growth and leaf area production in aspen and birch, such that these treatments did not generally differ significantly from controls. Maple showed an overall negative above-ground growth response to all treatments, but the variability was extremely high between individual saplings. As with photosynthesis, above-ground growth responses varied widely in magnitude among aspen genotypes. After 4 years of research at Aspen FACE, there are indications that the physiological and genetic responses, which were detected early in the experiment, are cascading through the ecosystem and resulting in significant ecosystem-level responses to CO_2 and O_3.

Wood and leaf biochemistry

O_3-induced stimulations of transcript production of several antioxidants were found and the same antioxidants appear to be down-regulated under elevated CO_2, regardless of O_3 exposure (see Karnosky *et al*., 2003). Furthermore, both CO_2 and O_3 induced decreases in transcripts of the small subunit of Rubisco and decreases in Rubisco concentrations. O_3-induced changes in chlorophyll concentrations were consistent with the degradation of chloroplasts. In aspen, the total lignin concentration in stem wood increased by 2.5% under elevated O_3 compared to the control, but otherwise no significant effects of CO_2 and/or O_3 on wood chemistry (a-cellulose, hemicellulose and acetone-soluble extractives) were observed (see Karnosky *et al*., 2003). In aspen and birch, foliar N concentrations declined by 16-21% in response to CO_2-enrichment, resulting in increased C:N ratios, but declined only marginally in response to elevated O_3 (Lindroth *et al*., 2001). The increased C:N ratio was maintained in litter, independent of O_3 concentration. Decreased N concentration in foliage under elevated CO_2 has been reported commonly for tree species (Cotrufo *et al*., 1998; Norby *et al*., 2000). Elevated CO_2 altered concentrations of C-based secondary metabolites in aspen and birch (Lindroth *et al*., 2001; Lindroth *et al*., 2002), but the direction and magnitude of responses differed among particular metabolites and between aspen clones. As with C:N ratios, secondary metabolite concentrations were highest in litter in CO_2-enriched atmosphere and lowest in high O_3 atmosphere (Karnosky *et al*., 2003). Elevated CO_2 and O_3 also altered rates of leaf epicuticular wax biosynthesis with increases and decreases depending on clone and treatment, modified amounts of C allocated to various wax forms, and changed chemical composition. O_3 modified wax structure from crystalline to amorphous masses (Mankovska *et al*., 1998) in aspen and birch, which may have contributed to increased incidences of the aspen leaf rust in O_3 and CO_2+O_3 treatments by altering the wettability of the leaf surface.

5. Impacts of ozone and climate change on weeds, pests and diseases

The occurrence of plant pests (weeds, insects or microbial pathogens) is an important constraint with global average yield losses estimated at about 40% (Oerke *et al*., 1994), and production costs significantly dependent on the extent of measures necessary for plant protection. Consequently, changes in the occurrence of pests due to climate change are of ecological and economical importance. Because insect and plant species show individual responses to climate change, it is expected that climate change will affect the temporal and spatial association between species interacting at different trophic levels (Harrington *et al*., 1999).

Weeds

Virtually nothing is known about effects of elevated O_3 on crop-weed interactions (see Fuhrer and Brooker, 2003), but O_3 may potentially affect the ability of weeds and crops to compete for common resources. In the case of aggressive weed species of tropical or subtropical origin, future climatic conditions may lead to their expansion into temperate regions. The generalized prediction that in a CO_2-rich world major crops will compete more successfully with the worst agricultural weeds, which are mostly C_4 species (Dukes and Mooney, 1999), may not be accurate due to regional differences. For instance, in the US, 9 out of 15 worst weeds in the most important crops are C_3, and a substantial fraction of crops are C_4 (Bunce and Ziska, 2000). The interactions between weeds and crops or grassland species in relation to climate change are complex and further experiments with different crop-weed systems under a range of atmospheric and edaphic conditions are needed to allow for accurate predictions.

Insect pests

It is generally expected that with climate warming in mid- to high-latitude regions insect pests become more abundant. The main effect of climate warming in the temperate zone is believed to be a change in winter survival, while in the northern latitude shifts in phenology in terms of growth and reproduction, may be of prime importance (Bale *et al*., 2002). Shifts in climate are also likely to affect the geographical distribution of insects. For instance, climate change may lead to a northwards shift in the potential distribution of insects (Patterson *et al*., 1999), although the expansions may be limited by the ability of the host plants to move. However, temperature effects may depend on photoperiod, and climate warming disturbs the synchrony between temperature and photoperiod. Extremes like droughts or floods are important triggers for the outbreak of insects within their habitat, and shifts in the probability of such trigger events may be an important aspect of climate change effects on agricultural ecosystems. The direct effects of temperature on insects are likely to differ among species, depending on their current environment, life-histories, and their ability to adapt (Bale *et al*., 2002), and given the many interactions between ecosystem processes, human influences, and environmental conditions, long-term predictions remain difficult.

Elevated CO_2 affects the chemical composition of leaves including increased C:N ratio, altered concentrations of allelochemicals, non-structural carbohydrates, starch and fibre content (Lincoln *et al*., 1993), or increased concentrations of substances involved in disease resistance (Idso and Idso, 2001), and can therefore affect insect herbivory. Bezemer and Jones (1998) concluded that leaf chewers can compensate for decreased N content by strongly increasing their food consumption, in contrast to leaf miners with only a small increase, and seed-eaters showing no effect. The response of leaves-sucking insects (e.g. mites) or phloem feeders (e.g. aphids) is species and host-plant dependent and can ranges from positive to negative (Bezemer *et al*., 1999; Fuhrer, 2003). At the whole plant level, the damaging effect of herbivores may be compensated by increased leaf production leading to increased rather than decreased photosynthetic performance in some species (Hughes and Bazzaz, 1997). Predictions about long-term population responses are difficult due to difference in the response to elevated CO_2 between different plant-insect combinations.

Species-specific responses of pests to increasing O_3 concentrations were observed (see Fuhrer, 2003). In contrast to elevated CO_2, O_3 tends to increase the N concentration in leaves (Pleijel *et al*., 1999). However, the relevant plant nutritive factor in the response of herbivores to O_3 might be the carbohydrate rather than the N concentration in leaves, as O_3 stress increases herbivore development as well as foliar sugar and starch in some host-plant systems (Heagle *et al*., 1994; Hummel *et al*., 1998).

Elevated CO_2 and O_3 may alter the performance of insects through changes in bottom-up (plant) and top-down (natural enemy) control. In Aspen FACE, CO_2 did not increase leaf foliar consumption by insects, in contrast to well established findings with potted aspen trees in greenhouses (Lindroth *et al*., 1993; Bezemer and Jones, 1998). Divergent pheromone-mediated behaviours could alter predator-prey interactions in future environment, e.g. *Chaitophorus stevensis*, a common aphid on trembling aspen trees (*Populus temuloides*), have diminished escape responses in enriched CO_2, but augmented escape responses to alarm pheromone in enriched O_3 atmosphere (Mondor *et al*., 2004). Elevated CO_2 and O_3 also have the potential to alter insect community composition. Increases in pest numbers may have considerable impact on forest health and productivity in the future. The importance of insect pest and disease eruptions in altering C fluxes from ecosystems has been highlighted by Kurz and Apps (1999), who detected a decade-long shift from carbon sink to source in the boreal forests of Canada due to increases in disturbance by pests and fire.

In summary, in an atmosphere containing higher levels of both O_3 and CO_2, increased populations of some insect pests can be expected.

Plant diseases

Impacts of climate change on specific host-pathogen systems are variable (Coakley *et al*., 1999; Chakraborty *et al*., 2000; see Fuhrer, 2003). In addition, O_3 effects on plants lead to altered disease susceptibility, but the effect is inconsistent. In wheat, leaf rust disease was strongly inhibited by O_3, but largely unaffected by elevated CO_2 both in the presence and absence of O_3 stress (Von Tiedemann and Firsching, 2000). O_3 damage to leaves was strongly affected by CO_2 concentration and infection. On infected plants, O_3 lesions appeared 2-4 weeks earlier and were up to fourfold more severe compared to non-infected plants. Elevated CO_2 did not delay the onset of lesions but it significantly reduced the severity of leaf damage. The relative increases in growth and yield induced by CO_2 were much larger on O_3-stressed than on non-stressed plants. Both O_3 and fungal infection reduced biomass formation and grain yield. However, adverse effects of leaf rust infection were more severe. Elevated CO_2 compensated for the negative effects of O_3 but not for the detrimental effects of fungal infection. Therefore, the impact of O_3 in the field should not be estimated without considering the predisposing effects deriving from fungal infections and the compensating effects deriving from elevated CO_2. The interaction between O_3 and pathogens may be determined primarily by the timing of O_3 exposure relative to the presence of inoculation. The outcome of plant-pathogen interactions may strongly vary with timing, stage of plant development, predisposing factors, and environmental conditions (Fuhrer, 2003).

6. Conclusions, policy implications and research needs

This review has revealed that there is currently much uncertainty in predicting the effects of O_3 in the changing climate of the 21st century. The Intergovernmental Panel on Climate Change has predicted changes in global mean temperature of 1.4 – 5.8 °C, an increase in CO_2 concentration to 540–970 ppm and altered precipitation patterns. Some generalised predictions can be made for each of these changes when studied in isolation, for example, elevated CO_2 will increase cereal crop productivity whilst increased temperature will decrease the productivity of cereals. However, in reality, within ecosystems, vegetation responses to climate change are driven by complex interactions between abiotic and biotic factors such as atmospheric CO_2, temperature, nutrient and water availability, atmospheric pollutants, soil characteristics, land-use/management and species composition/diversity, and therefore are difficult to predict (e.g. Shaw *et al.*, 2002; Beier, 2004; Harmens *et al.*, 2004). Responses to the individual drivers of climate change are highly species-specific and the behaviour of species responses within ecosystems to these environmental changes can often not be predicted from responses by isolated plants (see Fuhrer *et al.*, 2003 and Harmens *et al.*, 2004). When the changes in mean global O_3 concentration from -12 to +62% (IPCC, 2001a) with changing profile (decreased peak with increasing background concentrations) are also brought into the predictions for the 21st century, the scope for generalising responses within this review is rather limited.

6.1 Policy implications

When considering the policy implications of the effects of O_3 in a changing climate, the following sources of uncertainty need to be taken into account:

- *Plant responses to climate change (including elevated O_3 concentrations) are species-specific and sometimes even cultivar-specific, and are influenced by other factors such as local climate, soil characteristics and management.* The species-specific sensitivity means that effects on plant community structure and biodiversity are likely.
- *Vegetation responses to changes in single drivers of climate change cannot simply be scaled up to predict responses to changes in multiple drivers.* For example, whilst a rise in CO_2 concentration would be expected to reduce stomatal opening and thus reduce O_3 uptake, the reduced g_s will increase leaf temperature due to a reduction in cooling of the leaves by evapotranspiration, which adds to an enhanced affect of temperature on conductance (response to increased temperature can be increased or decreased depending if the leaf temperature is below or above the optimum for the species studied, respectively).
- *The responses from individual pot experiments in controlled environmental chambers can often not simply be scaled up to responses at ecosystem level at the field scale.*
- *Results from field release (FACE) systems provide the most reliable information on plant responses to combinations of drivers.* Although FACE studies generally substantiate predictions based on chamber studies, some inconsistencies between the results of chamber and FACE studies have been reported. Results from chamber-based experiments might both over- (e.g. crops) and underestimate (e.g. trees) ecosystem responses to environmental changes. The main disadvantage of FACE systems is the very high cost of running them, with costs for CO_2 being in the order of ten times those for O_3.

Taking into account the uncertainties described above and the currently availability of information, the following conclusions can be tentatively drawn at this stage on the responses to O_3 in a changing climate:

- *There is a tendency for O_3 effects to be less pronounced at elevated CO_2.* This effect has been detected in soybean, cotton, maize, potato and wheat, and in the Aspen FACE system, O_3 treatment offset the beneficial effect of CO_2 in both O_3-sensitive and -resistant clones of three tree species. CO_2-induced reduction in the stomatal uptake of O_3 is believed to be responsible for this beneficial effect.
- *Global warming may reduce the ameliorating effect of elevated CO_2 on the response to O_3.* Under conditions of no water stress, at a temperature below the optimum for the species concerned, warming is likely to increase O_3 uptake whilst a rise in elevated CO_2 is likely to decrease uptake.
- *The combined drivers of climate change will influence the flux of O_3 into leaves and will thus influence the magnitude of effect for a given atmospheric concentration.* The magnitude and direction of effect on flux will depend on the combined response to temperature, CO_2 concentration, vapour pressure deficit, soil moisture content, O_3 concentration and plant development stage at any moment in time.
- *There is no conclusive evidence that elevated CO_2 will increase the rate of O_3 detoxification within plants.* Responses appear to be species-species specific, with more studies showing no effect than studies showing an increasing detoxification of O_3. There is the generalized conclusion that the beneficial effects of CO_2 in reducing O_3 effect are stomatal rather than detoxification mediated.
- *Responses of insects and pathogens to the combined effects of elevated CO_2 and O_3 are species-specific.* By altering leaf chemistry, both O_3 and CO_2 can enhance insect and pathogen attack in some species.
- *Elevated O_3 at relatively low concentrations can significantly reduce the growth enhancement by elevated CO_2 and therefore reduce C sequestration*. This may mean that worldwide growth stimulations will not be as great as predicted from previous studies of elevated CO_2. Thus, it is important to bring an understanding of O_3 as a moderator of CO_2 responses in global models of terrestrial net primary productivity and C sequestration. The situation is even more complicated when plant-plant and plant-herbivore interactions or feedbacks operating through the soil are considered.

6.2 Research recommendations

- The influence of climate change should be taken into account when predicting the future effects of O_3 on vegetation.

- In the first instance, the O_3-flux modelling procedures outlined in the Mapping Manual (LRTAP Convention, 2004) will need revising to include CO_2 concentration as a modifying factor.

- In the longer-term, it may be necessary to develop alternative modelling procedures since the current method is based on the stomatal responses to climatic and plant factors considered in isolation rather than in combination.

- There is a clear need for multi-factorial experiments to provide information for O_3-effect modelling. Because of the high cost involved with FACE systems, these may only be possible using enclosed or semi-enclosed chamber systems especially where warming and CO_2 are considered as factors.

- As very little is known about the vulnerability of communities of (semi-)natural vegetation to O_3 and climate change, there is an urgent need for experiments that enhance our understanding of their impacts on vegetation responses and species competition. With little information available, much progress could be made in the short-term by conducting experiments with closed or semi-enclosed exposure systems. Despite the higher costs and increased complexity, the longer-term aim should be to conduct FACE experiments to assess the vulnerability of (semi-)natural vegetation to O_3 and climate change.

- There is a need for a wider and longer-term use of FACE for crops and forest trees to expand the range of species for which data exists and to determine the cumulative effects over several years.

- So far, FACE experiments have focussed on temperate ecosystems, while tropical, boreal and arctic systems have been largely ignored. FACE experiments with tropical forests, representing 50% of C in terrestrial biomass, are an obvious international need.

7. References

Ainsworth, E.A., Long, S.P. (2005). What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* 165, 351-372.

Ali M., Jensen C.R., Mogensen V.O., Andersen M.N., Hensen I.E. (1999). Root signalling and osmotic adjustment during intermittent soil drying sustain grain yield of field grown wheat. *Field Crops Research* 62, 35-52.

Amthor, J.S. (2001). Effects of atmospheric CO_2 concentration on wheat yield: review of results from experiments using various approaches to control CO_2 concentration. *Field Crops Research* 73, 1-34.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittacker, J.B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8, 1-16.

Basu, P.S., Sharma, A., Garg, I.D., Sukumaran, N.P. (1999). Tuber sink modifies photosynthetic response in potato under water stress. *Environmental and Experimental Botany* 42, 25-39.

Batts, G.R., Morison, J.I.L., Ellis, R.H. Hadley, P., Wheeler, T.R. (1997). Effects of CO_2 and temperature on growth and yield of crops of winter wheat over several seasons. *European Journal of Agronomy* 7, 43-52.

Beier, C. (2004). Climate change and ecosystem function – full-scale manipulations of CO_2 and temperature. *New Phytologist* 162, 243-245.

Bender J., Hertstein, U., Black, C.R. (1999). Growth and yield responses of spring wheat to increasing carbon dioxide, ozone and physiological stresses: a statistical analysis 'ESPACE-wheat' results. *European Journal of Agronomy* 10, 185-195.

Bezemer, T.M., Jones, T.H. (1998). Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. *Oikos* 82, 212-222.

Bezemer, T.M., Knight, K.J., Newington, J.E., Jones, T.H. (1999). How general are aphid responses to elevated atmospheric CO_2? *Annals of Entomological Society of America* 92, 724-730.

Bunce, J.A. (2000). Responses of stomatal conductance to light, humidity and temperature in winter wheat and barley grown at three concentrations of carbon dioxide in the field. *Global Change Biology* 6, 371-382.

Bunce, J.A., Ziska, L.H. (2000). Crop ecosystem responses to climatic change: crop/weed interactions. In: Reddy, K.R., Hodges, H.F. (eds.). *Climate Change and Global Crop Productivity*. CABI Publishing. Wallingford, U.K. pp. 333-352.

Campbell, B.D., Stafford Smith, M.D., McKeon, G.M. (1997). Elevated CO_2 and water supply interactions in grasslands: a pasture and rangelands management perspective. *Global Change Biology* 3, 177-187.

Chakraborty, S., Tiedemann, A.V., Teng, P.S. (2000). Climate change: potential impact on plant diseases. *Environmental Pollution* 108, 317-326.

Coakley, S.M., Scherm, H., Chakraborty, S. (1999). Climate change and plant disease management. *Annual Review of Phytopathology* 37, 399-426.

Cotrufo, M.F., Ineson, P., Scott, A. (1998). Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biology* 4, 43-54.

Craigon, J., Fangmeier, A., Jones, M., Donnelly, A., Bindi, M., De Temmerman, L., Persson, K., Ojanpera, K. (2002). Growth and marketable-yield responses of potato to increased CO_2 and ozone. *European Journal of Agronomy* 17, 273-289.

Curtis, P.S., Wang, X. (1998). A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia* 113, 299-313.

Danielsson, H., Pihl Karlsson, G., Karlsson, P.E., Pleijel, H. (2003). Ozone uptake modelling and flux-response relationships – an assessment of ozone-induced yield loss in spring wheat. *Atmospheric Environment* 37, 475-485.

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

Drake, B.G., Gonzàlez-Meler, M.A., Long, S.P. (1997). More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology* 48, 609-639.

Dukes, J.S., Mooney, H.A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14, 135-139.

Dwelle, R.B., Hurley, P.J., Pavek, J.J. (1983). Photosynthesis and stomatal conductance of potato clones (*Solanum tuberosum* L.). *Plant Physiology* 72, 172-176.

Emberson, L.D. (1997). *Defining and mapping relative potential sensitivity of European vegetation to ozone.* Imperial College, University of London. PhD Thesis.

Emberson, L.D., Ashmore, M.R., Cambridge, H.M., Simpson, D., Tuovinen, J.-P. (2000). Modelling stomatal ozone flux across Europe. *Environmental Pollution* 109, 403-413.

Fangmeier, A., Chrost, B., Hogy, P., Krupinska, K. (2000). CO_2 enrichment enhances flag leaf senescence in barley due to greater grain nitrogen sink capacity. *Environmental and Experimental Botany* 44, 151-164.

Fangmeier, A., De Temmerman, L., Mortensen, L., Kemp, K., Burke, J., Mitchell, R., Van Oijen, M., Weigel, H.J. (1999). Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO_2 concentrations and stress conditions in the European, multiple-site experiment 'Espace-wheat'. *European Journal of Agronomy* 10, 215-229.

Farage, P.K., Long, S.P. (1992). Ozone inhibition of photosynthesis — a mechanistic analysis following short-term and long-term exposure in 3 contrasting species. *Photosynthesis Research* 34, 244-254.

Fiscus, E.L., Reid, C.D., Miller, J.E., Heagle, A.S. (1997). Elevated CO_2 reduces O_3 flux and O_3-induced yield losses in soybeans: possible implications for elevated CO_2 studies. *Journal Experimental Botany* 48, 307-313.

Fuhrer, J. (2003). Agroecosystem reponses to combinations of elevated CO_2, ozone, and global climate change. *Agriculture, Ecosystems and Environment* 97, 1-20.

Fuhrer, J., Achermann B. (eds.) (1994). *Critical levels for ozone – level II*. Swiss Agency for the Environment, Forests and Landscape, Berne. Environmental Documentation No. 115.

Fuhrer, J., Ashmore, M.R., Mills, G., Hayes, F., Davison, A.W. (2003). Critical levels for semi-natural vegetation. In: Karlsson, P.E., Selldén, G., Pleijel, H., (eds). (2003). *Op. cit.*

Fuhrer, J., Booker, F. (2003). Ecological issues of ozone: agricultural issues. *Environment International* 29, 141-154.

Fuhrer, J., Grandjean Grimm, A., Tschannen, W., Shariat-Madari, H. (1992). The response of spring wheat (*Triticum aestivum* L.) to ozone at higher elevations. II Changes in yield, yield components and grain quality in response to ozone flux. *New Phytologist* 121, 211-219.

Fuhrer, J., Lehnherr, B., Moeri, P.B., Tschannen, W., Shariat-Madari, H. (1990). Effects of ozone on the grain composition of spring wheat grown in open-top field chambers. *Environmental Pollution* 65, 181-192.

Gaucher, C., Costanzo, N., Afif, D., Maufette, Y., Chevrier, N., Dizengremel, P. (2003). The impacts of elevated ozone and carbon dioxide on young *Acer saccharum* seedlings. *Physiologia Plantarum* 117: 392-402.

Gollan, T., Passioura, J.B., Munns, R. (1986). Soil water status effects the stomtal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology* 13, 459-464.

Grandjean, A., Fuhrer, J. (1989). Growth and leaf senescence in spring wheat (*Triticum aestivum* L. CV. Albis) grown at different ozone concentrations in open-top field chambers. *Physiologia Plantarum* 77, 389-394.

Grantz., D.A., Farrar, J.F. (1999). Acute exposure to ozone inhibits rapid carbon translocation from source leaves of pima cotton. *Journal of Experimental Botany* 50, 1253-1262.

Grantz, D.A., Yang, S.Y. (2000). Ozone impacts on allometry and root hydraulic conductance are not mediated by source limitation nor developmental age. *Journal of Experimental Botany* 51, 919-927.

Gruters, U., Fangmeier, A., Jager, H.-J. (1995). Modelling stomatal responses of spring wheat (*Triticum aestivum* L. cv. Turbo) to ozone at different levels of water supply. *Environmental Pollution* 87, 141-149.

Harmens, H., Williams, P.D., Peters, S.L., Bambrick, M.T., Ashenden, T.W., Hopkins, A. (2004). Impacts of elevated atmospheric CO_2 and temperature on plant community structure in a temperate grassland are modulated by cutting frequency. *Grass and Forage Science* 59, 144-156.

Harrington, R., Woidwood, I., Sparks, T. (1999). Climate change and trophic interactions. *Trends in Ecology and Evolution* 14, 146-150.

Heagle A.S., Miller, J.E., Booker, F.L., Pursley, W.A. (1999). Ozone stress, carbon dioxide enrichment, and nitrogen fertility interactions in cotton. *Crop Science* 39, 731-741.

Heagle, A.S., Miller, J.E., Pursely, W.A. (1998). Influcence of ozone stress on soybean response to carbon dioxide enrichment. III. Yield and seed quality. *Crop Science* 38, 128-134.

Heagle, A.S., Miller, J.E., Pursley, W.A. (2000). Effects of ozone and carbon dioxide interactions on growth and yield of winter wheat. *Crop Science* 40, 1656-1664.

Heagle, A.S., Miller, J.E., Sherrill, D.E., Rawlings, J.O. (1993). Effects of ozone and carbon dioxide mixtures on 2 clones of white clover. *New Phytologist* 123, 751-762.

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

Hendrey, G.R., Lewin, K.F., Nagy, J. (1993). Free air carbon dioxide enrichment: development, progress, results. *Vegetatio* 104/105, 17-31.

Hughes, L., Bazzaz, F.A. (1997). Effect of elevated CO_2 on interactions between the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae) and the common milkweed, *Asclepias syriaca. Oecologia* 109, 286-290.

Hui, D.F., Luo, Y.Q., Cheng, W.X., Coleman, J.S., Johnson, D.W., Sims, D.A. (2001). Canopy radiation – and water-use efficiencies as affected by elevated CO_2. *Global Change Biology* 7, 75-91.

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R., Hill, S. (2002). *Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report*. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK.

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

Idso, S.B., Idso, K.E. (2001). Effects of atmospheric CO_2 enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* 45, 179-199.

IPCC (2001a). *Climate change 2001: The scientific basis*. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change (eds. J.T. Houghton *et al*.). Cambridge University Press, Cambridge, UK and New York, NY, USA.

IPCC (2001b). *Climate change 2001: Impacts, adaptation and vulnerability*. Contribution of Working Group 2 to the Third Assessment Report of the Intergovernmental Panel on Climate Change (eds. J.J. McCarthy *et al*.). Cambridge University Press, Cambridge, UK and New York, NY, USA.

Kang, S.Z., Zhang, F.C., Hu, X.T., Zhang, J.H. (2002). Benefits of CO_2 enrichment on crop plants are modified by soil water status. *Plant Soil* 238, 69-77.

Kärenlampi, L., Skärby, L. (eds.) (1996). *Critical levels for ozone in Europe: testing and finalizing the concepts* (UN/ECE Workshop Report). University of Kuopio, Dept. of Ecology and Environmental Science, Kuopio, Finland.

Karlsson, P.E., Selldén, G., Pleijel, H., (eds). (2003). *Establishing ozone critical levels II.* UNECE Workshop Report. IVL report B 1523. IVL Swedish Environmental Research Institute, Gothenburg, Sweden. http://www.ivl.se

Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R., Sober, A., Sober, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W., Isebrands, J.G. (2003). Tropospheric O_3 moderates responses of temperate hardwood forests to elevated CO_2: a synthesis of molecular to ecosystem results from the Aspen FACE project. *Functional Ecology* 17, 289-304.

Kimball, B.A., Kobayashi, K., Bindi, M. (2002). Responses of agricultural crops to free-air CO_2 enrichment. *Advances in Agronomy* 77, 293-368.

King, J.S., Pregitzer, K.S., Zak, D.R., Sôber, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., Karnosky, D.F. (2001). Fine root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. *Oecologia 128*, 237-250.

Kollist, H., Moldau, H., Mortensen, L., Rasmussen, S.K., Jorgensen, L.B. (2000). Ozone flux to plasmalemma in barley and wheat in controlled by stomata rather than by direct reaction of ozone with cell wall ascorbate. *Journal of Plant Physiology* 156, 645-651.

Ku, S.-B., Edwards, G.E., Tanner, C.B. (1977). Effects of light, carbon dioxide and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in *Solanum tuberosum*. *Plant Physiology* 59, 868-872.

Kubiske, M.E., Godbold, D.L. (2001). *Influence of carbon dioxide on the growth and function of roots and root systems. The impacts of carbon dioxide and other greenhouse gases on forest ecosystems* (eds. D.F. Karnosky, G. Scarscia-Mugnozza, R. Ceulemans, J. Innes). CABI Publishing, Wallingford, UK. pp. 297-324.

Kurz, W.A., Apps, M.J. (1999). A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecology Applications* 9, 526-547.

Leakey, A.D.B., Bernacchi, C.J., Dohleman, F.G., Ort, D.R., Long, S.P. (2004) Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO_2] rich atmospheres? An analysis of diurnal courses of CO_2 uptake under free-air concentration enrichment (FACE). *Global Change Biology* 10, 951-962.

Lee, E.H. (2000). Early detection, mechanisms of tolerance, and amelioration of ozone stress in crop plants. In: Agrawal, S.B., Agrawal, M. (eds.), *Environmental pollution and plant responses*. CRC Press, Boca Raton, FL, pp. 203-222.

Lehnherr, B., Grandjean, A., Mächler, F., Fuhrer, J. (1997). The effect of ozone in ambient air on ribulose bisphophate carboxylase/oxygenase activity decreases photosynthesis and grain yield in wheat. *Journal of Plant Physiology* 130, 189-200.

Leipner, J., Oxborough, K., Baker, N.R. (2001). Primary sites of ozone induced perturbations of photosynthesis in leaves: identification and characterization in *Phaseolus vulgaris* using high resolution chlorophyll fluorescence imaging. *Journal of Experimental Botany* 52, 1689-1696.

Lincoln, D.E., Fajer, E.D., Johnson, R.H. (1993). Plant insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution* 8, 64-68.

Lindroth, R.L., Kinney, K.K., Platz, C.L. (1993). Responses of deciduous trees to elevated atmospheric CO2: productivity, phytochemistry and insect performance. *Ecology* 74, 763-777.

Lindroth, R.L., Kopper, B.J., Parsons, W.F.J., Bockheim, J.G., Sôber, J., Hendrey, G.R., Pregitzer, K.S., Isebrands, J.G., Karnosky, D.F. (2001). Effects of elevated carbon dioxide and ozone on foliar chemical composition and dynamics in trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). *Environmental Pollution* 115, 394-404.

Lindroth, R.L., Wood, S.A., Kopper, B.J. (2002). Response of quaking aspen genotypes to enriched CO_2: foliar chemistry and tussock moth performance. *Agricultural and Forest Entomology* 4, 315-323.

LRTAP Convention (2004). *Manual on methodologies and criteria for modelling and mapping critical loads & levels and air pollution effects, risks and trends*. Convention on Long-range Transboundary Air Pollution. http://www. icpmapping.org

Mankovska, B., Percy, K., Karnosky, D.F. (1998). Impact of ambient tropospheric O_3, CO_2 and particulates on the epicuticular waxes of aspen cones differing in O_3 tolerance. *Ekológia* 18, 200-210.

Marabottini, R., Schraml, C., Paolacci, A.R., Sorgona, A., Rachi, A., Rennenberg, H., Badiani, M. (2001). Foliar antioxidant status of adult Mediterranean oak species (*Quercus ilex* L. and *Q. pubescens* Willd.) exposed to permanent CO_2-enrichment and to seasonal water stress. *Environmental Pollution* 115, 413-423.

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

McKee, I.F., Eiblmeier, M., Polle, A. (1997). Enhanced ozone-tolerance in wheat grown at an elevated CO_2 concentration: ozone exclusion and detoxification. *New Phytologist* 137, 275-284.

McLeod, .A.R., Long, S.P. (1999). Free air carbon dioxide enrichment (FACE) in global change research: a review. *Advances in Ecological Research* 28, 1-55.

Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P., Forstreuter, M., Freeman, M., Jackson, S.B., Kellomaki, S., Laitat, E., Rey, A., Roberntz, P., Sigurdsson, B.D., Strassemeyer, J., Wang, K., Curtis, P.S., Jarvis, P.G. (2001). Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentrations: a synthesis. *New Phytologist* 149, 247-264.

Mills, G., Holland, M., Buse, A., Cinderby, S, Hayes, F., Emberson, L., Cambridge, H., Ashmore, M., Terry, A. (2003). Introducing response modifying factors into a risk assessment for ozone effects on crops in Europe. In: Karlsson, P.E., Selldén, G., Pleijel, H. (eds). (2003). *Op. cit.*

Mills, G., Harmens, H., Hayes, F., Williams, P., Emberson, L., Cinderby, S., Terry, A., Ashmore, M., Holland, M., Green, E., Power, S. (2005). *The UNECE International Cooperative Programme on Vegetation*. Defra contract EPG 1/3/205. Progress Report (April, 2004 – March, 2005). ICP Vegetation Coordination Centre, Centre for Ecology and Hydrology, Bangor, UK.

Mondor, E.B., Tremblay, M.N., Awmack, C.S., Lindroth, R.L. (2004). Divergent pheromone-mediated insect behaviour under global atmospheric change. *Global Change Biology* 10, 1820-1824.

Morgan, J.A. (1984) Interaction of water supply and N in wheat. *Plant physiology* 76, 112-117.

Morgan, J.A., LeCain, .D.R., Mosier, A.R., Milchunas, D.G. (2001). Elevated CO_2 enhances water relations and productivity and affects gas exchange in C-3 and C-4 grasses of the Colorado shortgrass steppe. *Global Change Biology* 7, 451-466.

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

NEGTAP (2001). *Transboundary air pollution: acidification, eutrophication and ground-level ozone in the UK*. DEFRA Contract no. EPG 1/3/153, UK.

Niewiadomska, E., Gaucher-Veilleux, C., Chevrier, N., Maufette, Y., Dizengremel, P. (1999). Elevated CO_2 does not provide protection against ozone considering the activity of several antioxidant enzymes in the leaves of suger maple. *Journal of Plant Physiology* 155, 70-77.

Nijs, I., Teughels, H., Blum, H., Hendrey, G., Impens, I. (1996). Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L. in summer. *Environmental and Experimental Botany* 36, 271-280.

Noormets, A., Sober, A., Pell, E.J., Dickson, R.E., Podila, G.K., Sober, J., Isebrands, J.G., Karnosky, D.F. (2001a). Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO_2 and/or O_3. *Plant, Cell and Environment* 24, 327-336.

Noormets, A., McDonald, E.P., Kruger, E.L., Sober, A., Isebrands, J.G., Dickson, R.E., Karnosky, D.F. (2001b). The effect of elevated carbon dioxide and ozone on leaf-and branch-level photosynthesis and potential plant-level carbon gain in aspen. *Trees: Structure and Function* 15, 262-270.

Norby, R.J., Long, T.M., Hartz-Rubin, J.S., O'Neill, E.G. (2000). Nitrogen resorption in senescing tree leaves in a warmer, CO_2-enriches atmosphere. *Plant and Soil* 224, 15-29.

Norby, R.J., Luo, Y. (2004). Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. *New Phytologist* 162, 281-293.

Norby, R.J., Todd, D.E., Fults, J., Johnson, D.W. (2001). Allometric determination of tree growth in a CO_2-enriched sweetgum stand. *New Phytologist* 150, 477-487.

Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R. (1999). Tree responses to rising CO_2 in field experiments: implications for the future forest. *Plant, Cell and Environment* 22, 683-714.

Nowak, R.S., Ellsworth, D.S., Smith, S.D. (2004). Functional responses of plants to elevated atmospheric CO2 – do photosynthetic and productivity data from FACE experiments support early prediction. *New Phytologist* 162, 253-280.

Oerke, E.C., Dehne, H.W., Schönbeck, F., Weber, A. (1994). *Crop production and crop protection: estimated losses in major food and cash crops*. Elsevier, Amsterdam.

Ollerenshaw, J.H., Lyons, T., Barnes, J.D. (1999). Impacts of ozone on the growth and yield of field-grown winter oilseed rape. *Environmental Pollution* 104, 53-59.

Oren, R., Ellsworth, D.S., Johnson, K.H. Phillips, N., Ewers, B.E., Maier, C., Schafer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G.G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature* 411, 469-472.

Owensby, C.E. Ham, J.M., Knapp, A.K., Auen, L.M. (1999). Biomass production and species composition change in a tall grass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology* 5, 497-506.

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

Patterson, D.T., Westbrook, J.K., Joyce R.J.V., Lingren, P.D., Rogasik, J. (1999). Weeds, insects, and diseases. *Climatic Change* 43, 711-727.

Pell, E.J., Eckardt, N.A., Glick, R.E. (1994). Biochemical and molecular basis for the impairment of photosynthetic potential. *Photosynthesis Research* 39, 453-462.

Peñuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B.A., Estiarte, M., Gorissen, T. (2004). Non-intrusive field experiments show different plant responses to warming and drought among sites, season and species in a North-South European gradient. *Ecosystems* 7, 598-612.

Pleijel, H., Danielsson, H., Vandermeiren, K., Blum, C., Colls, J., Ojanperä, K. (2002). Stomatal conductance and ozone exposure in relation to potato tuber yield – results from the European CHIP programme. *European Journal of Agronomy* 17, 303-317.

Pleijel, H., Gelang, J., Sild, E., Danielsson, H., Younis, S., Karlsson, P.E., Wallin, G., Skarby, L., Sellden, G. (2000). Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield. Physiologia Plantarum 108, 61-70.

Pleijel, H., Mortensen, L., Fuhrer, J., Ojanperä, K., Danielsson, H. (1999). Grain protein accumulation in relation to grain yield of spring what (*Triticum aestivum* L.) grown in open-top chambers with different concentrations of ozone, carbon dioxide and water availability. *Agriculture, Ecosystems and Environment* 72, 265-270.

Porter, H., Perez-Soba, M. (2001). The growth response of plants to elevated CO_2 under non-optimal environmental conditions. *Oecologia* 129, 1-20.

Rao, M.V., Hale, B.A., Ormrod, D.P. (1995). Amelioration of ozone-induced oxidative damage in wheat plants grown under high carbon dioxide – role of antioxidant enzymes. *Plant Physiology* 109, 421-432.

Riedo, M., Gyalistras, D., Fischlin, A., Fuhrer, J. (1999). Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO_2 on dry matter production and partitioning, and water use in temperate managed grasslands. *Global Change Biology* 5, 213-223.

Robinson, J.M., Sicher, R.C. (2004). Antioxidant levels decrease in primary leaves of barley during growth at ambient and elevated carbon dioxide levels. *International Journal of Plant Sciences* 165, 965-972.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchel, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543-562.

Saurer, M., Fuhrer, J., Siegenthaler, U. (1991). Influence of ozone on the stable carbon isotope composition $8^{13}C$, of leaves and grain of spring wheat (*Triticum aestivum* L.). *Plant Physiology* 97, 313-316.

Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A., Field, C.B. (2002). Grassland responses to global environmental changes suppressed by elevated CO_2. *Science* 298, 1987-1990.

Sild, E., Pleijel, H., Sellden, G. (2002). Elvated ozone (O_3) alters carbohydrate metabolism during grain filling in wheat (*Triticum aestivum* L.). *Agriculture, Ecosystems and Environment* 92, 71-81.

Soja, G., Reichenauer, T.G., Eid, M., Soja, A.-M., Schaber, R., Gangl, H. (2004). Long-term ozone exposure and ozone uptake of grapevines in open-top chambers. *Atmospheric Environment* 38, 2313-2321.

Tjoelker, M.G., Oleksyn, J., Reich, P.B. (1998). Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. *Tree Physiology* 18, 715-726.

di Toppi, L.S., Marabottini, R., Badiani, M., Raschi, A. (2002). Antioxidant status in herbaceous plants growing under elevated CO_2 in mini-FACE rings. *Journal of Plant Physiology* 159, 1005-1013.

Tuebner, F. (1985). *Messung der Photosynthese und Transpiration an Weizen, Kartoffel und Sonnenblume*. Diplomarbeit University Bayreuth, West Germany.

Vandermeiren, K., Black, C., Lawson, T., Casanova, M.A., Ojanperä, K. (2002). Photosynthetic and stomatal responses of potatoes grown under elevated CO_2 and/or O_3 – results from the European CHIP-programme. *European Journal of Agronomy* 17, 337-352.

Van Oijen, M., Schapendonk, A.H.C.M., Jansen, M.J.H., Pot, C.S., Maciorowski, R. (1999). Do open-top chambers overestimate the effects of rising CO2 on plants? An analysis using spring wheat. *Global Change Biology* 5, 411-421.

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

Vorne, V., Ojanperä, K., De Temmerman, L., Bindi, M., Högy, P., Jones, M., Lawson, T., Persson, K. (2002). Effects of elevated carbon dioxide and ozone on patato tuber quality in the European multiple-site experiment CHIP-project. *European Journal of Agronomy* 17, 369-381.

Vos, J., Oyarzun, P.J. (1987). Photosynthesis and stomatal conductance of potato leaves - effects of leaf age, irradiance, and leaf water potential. *Photosynthesis Research* 11, 253-264.

Vozzo, S.F., Miller, J.E., Pursley, W.A., Heagle, A.S. (1995). Atmospheric pollutants and trace gases—effects of ozone and water-deficit on field-grown soybean. 1. Leaf gas-exchange. *Journal of Evironmental Quality* 24, 663-670.

Weber, P., Rennenberg, H. (1996). Dependency of Nitrogen dioxide (NO_2) fluxes to wheat (*Triticum aestivum* L.) leaves from NO_2 concentration, light intensity, temperature and relative humidity determined from controlled dynamic chamber experiments. *Atmospheric Environment* 30, 3001-3009.

Working Group on Effects, Convention on Long-range Transboundary Air Pollution (2004). *Review and assessment of air pollution effects and their recorded trends*. Working

Group on Effects, Convention on Long-range Transboundary Air Pollution. Natural Environment Research Council, UK. ISBN 1 870393 77 5.

Wustman, B.A., Oksanen, E., Karnosky, D.F., Sôber, J., Isebrands, J.G., Hendrey, G.R., Pregitzer, K.S., Podila, G.K. (2001). Effects of elevated CO_2 and O_3 on aspen clones varying in O_3 sensitivity: can CO_2 ameliorate the harmful effects of O_3? *Environmental Pollution* 115, 473-481.

Zhang, J., Xiangzhen, S., Li, B., Su, B., Li, J., Zhou, D. (1998). An improved water-use efficiency for winter wheat grown under reduced irrigation. *Field Crops Research* 59, 91-98.