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Assessing the future global impacts of ozone on vegetation

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ABSTRACT

Ozone is a major secondary air pollutant, the current concentrations of which have been shown to have significant adverse effects on crop yields, forest growth and species composition. In North America and Europe, emissions of ozone precursors are decreasing but in other regions of the world, especially Asia, where much less is known about its impacts, they are increasing rapidly. There is also evidence of an increase in global background ozone concentrations, which will lead to significant changes in global ozone exposure over this century, during which direct and indirect effects of other changes in the global atmosphere will also modify plant responses to ozone. This paper considers how far our current understanding of the mechanisms of ozone impacts, and the tools currently used for ozone risk assessment, are capable of evaluating the consequences of these changing global patterns of exposure to ozone. Risk assessment based on relationships between external concentration and plant response is inadequate for these new challenges. New models linking stomatal flux, and detoxification and repair processes, to carbon assimilation and allocation provide a more mechanistic basis for future risk assessments. However, there are a range of more complex secondary effects of ozone that are not considered in current risk assessment, and there is an urgent need to develop more holistic approaches linking the effects of ozone, climate, and nutrient and water availability, on individual plants, species interactions and ecosystem function.

Key-words: crops; flux; forests; global change; ozone; risk assessment; vegetation.

INTRODUCTION

Ozone is a major secondary air pollutant, produced by a complex series of photochemical reactions from primary precursor emissions of nitrogen oxides (NOx) and volatile organic compounds (VOCs). High concentrations of ozone are associated with hot sunny weather and occur over wide areas. The adverse effects of ozone on plants were first identified in the 1950s, and it is now recognized as the most important rural air pollutant, affecting human health and materials, as well as vegetation. Many articles (e.g. Davison & Barnes 1998; Ashmore 2002; Fuhrer & Booker 2003; Karlsson, Sellden & Pleijel 2003a; Matyssek & Sandermann 2003) have provided an overview of the impacts of ozone. The intention of this paper is to identify critical issues related to our understanding of the effects of changing patterns of ozone exposure in the specific context of a changing global environment, and to consider the implications of these changes for risk assessments of the future impacts of ozone.

The global patterns of exposure of vegetation to ozone are changing. Control measures on emissions of NOx and VOCs applied in North America and western Europe, where the impacts of ozone on crop production and forest vitality have been well established, are expected to lead to reductions in peak ozone concentrations. At the same time, global background tropospheric concentrations may be increasing as a result of human activities, and in particular increased global emissions of nitrogen oxides. Indeed there is already evidence of such a trend in long-term monitoring records. In the UK, for example, NEGTAP (2001) identified a 30% decline in peak concentrations over the past decade, probably due to reduced regional precursor emissions, but an increase in annual mean concentrations of 0.1 ppb per year. The predicted increases in global background ozone concentrations may reduce, or even negate, the impacts of regional emission control policies to reduce ozone concentrations. Furthermore, in parts of Asia, Latin America and Africa, predicted increases in global background concentrations are combined with trends of increased emissions of ozone precursors, suggesting that current and future ozone impacts on crops and forests in these areas may be very significant (Emberson *et al*. 2001, Emberson, Ashmore &Murray 2003). The economic and social implications of widespread loss of yield of staple crops, in regions where there are problems in maintaining food supplies in the face of rapidly increasing populations and loss of productive land, could be very serious (Ashmore & Marshall 1999).

Several studies have used global models to examine the impacts of continued increased emissions of nitrogen oxides on future ozone concentrations (e.g. Collins *et al*. 2000). Studies of background ozone concentrations in the mid-latitude northern hemisphere suggest an increase of 0.5–2% per year (Vingarzan 2004), which modelling studies suggest is primarily due to rising NOx emissions, augmented by intercontinental transport. Hence assessment of impacts on vegetation, and the effects of emission control policies, for ozone needs increasingly to be considered as a global as well a regional issue (Coyle, Fowler & Ashmore 2003). Figure 1 (from Vingarzan 2004) combines historical, recent and projected mean surface ozone concentrations, showing the rise over the past century, and the projected rise over the next century. These are based on different IPCC scenarios, and predict either an increase to 70 ppb (well above the threshold for effects on a range of types of vegetation) by 2050

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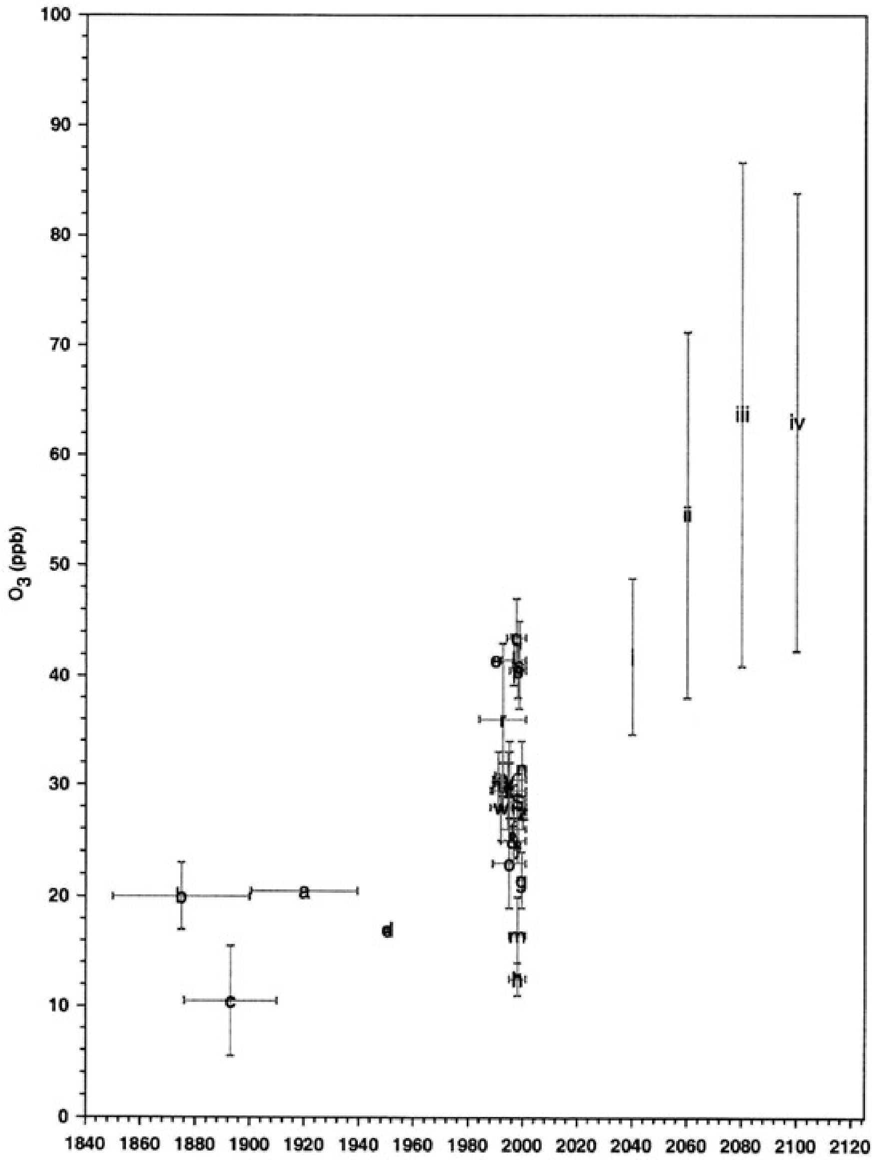

Figure 1. Historical, current and projected global background surface ozone annual mean concentrations. The range of projected concentrations reflects the range of different IPCC scenarios. From Vingarzan (2004).

under Business as Usual (BAU) scenarios to 'sustainability' scenarios under which the values stabilize at about 40 ppb.

The significance of these changes needs to be considered in the context of other predicted changes in global atmospheric composition and climate. There are important interactions with increasing CO_2 concentrations that may modify future ozone impacts, which are reviewed in detail elsewhere in this issue and will not be considered further in this paper. Changes in water availability, temperature and nutrient cycling may also interact with changing ozone exposure. Second-order interactions, for example, with the likelihood and severity of insect pest outbreaks, also need to be considered. Hence, as argued by Ashmore & Bell (1991), changing ozone concentrations are an important component of global change.

This paper aims to consider how far our current understanding of the mechanisms of ozone impacts on individual plants and on plant communities, and, in particular, current risk assessment methods, provide a sound basis for assessing the global implications of future changes in ozone exposure of vegetation. The paper first summarizes the evidence of impacts of ozone in different regions of the world, to assess the global scale of the problem. It then considers progress in risk assessment methods for ozone, which combine models of the spatial distribution of ozone exposures with exposure-response relationships to estimate the current and future impacts of ozone. Impacts of ozone that are poorly described in current risk assessment frameworks but which may be significant in the context of global change, such as those on carbon allocation and plant chemistry, are then considered. Finally, the paper considers the long-term impacts of ozone in the context of other environmental processes and stresses.

EFFECTS ON CROPS AND FORESTS: A GLOBAL OVERVIEW

Ozone can reduce agricultural yields by a variety of mechanisms. The first of these is acute visible injury, which for species with a market value dependent on their visible appearance, such as many horticultural crops, can cause an obvious and immediate loss of economic value. Ozone injury to crops has been commonly reported in North America and Europe, where the most severe damage is on irrigated crops in the Mediterranean region (Fumigalli *et al.* 2001). For example, an ozone episode north of Athens in 1998 caused such severe reddening and necrosis on *Chicorium endivum* and *Lactuca sativa* that local crops could not be sold (Velissariou 1999), with severe economic implications for local producers. There have been several reports of visible injury to crops caused by ozone outside North America and western Europe (Emberson *et al.* 2001,2003). These include injury to crops of *Phaseolus vulgaris* in Mexico (de Bauer 2003), radish (*Raphanus sativus*) and turnip (*Brassica rapa*) in Egypt (Hassan, Ashmore & Bell 1995), *Solanum tuberosum* in India (Bambawale 1986), and a range of horticultural crops in Taiwan (Sheu & Liu 2003).

These are isolated observations, often triggered by major impacts on local farmers, and there is little doubt that with appropriate systematic surveys, visible injury symptoms characteristic of ozone would prove to be more common than these reports indicate. In both North America and Europe, systematic surveys of visible injury in forests, supported by fumigation studies to replicate injury symptoms (Orendovici *et al.* 2003) and detailed microscopical analysis to confirm diagnosis (Vollenweider, Ottiger & Gunthardt-Goerg 2003a), have demonstrated widespread occurrence of injury on sensitive species (Chappelka *et al.* 1997; Skelly *et al.* 1999). Such surveys also reveal the effects of variation in site conditions, such as soil moisture levels; for example, Vollenweider *et al.* (2003b) found greater symptoms on *Prunus serotina* trees at higher elevation sites, with greater moisture availability and deeper soils.

Evidence of effects of ozone on forests outside Europe and the United States is very limited. The most extensively studied forest area is in the mountain areas outside Mexico City, where very high ozone concentrations are now recorded. Miller *et al.* (1994) reported that ozone exposures in these forests were comparable with those in the San Bernadino mountains outside Los Angeles, where extensive ozone damage has been documented. Visible foliar symptoms are commonly found in these areas (de Bauer 2003), on pine species such as *Pinus hartwegii* and *Pinus montezumae*, on sacred fir (*Abies religiosa*), and on *Prunus serotina*, while dendrochronological analysis has shown clear evidence of a growth decline since the early 1970s (Alvarado, Bauer & Galindo 1993).

Ozone can reduce the marketable yield of a range of crop species, in the absence of visible injury, primarily through its effects in reducing photosynthetic rates and accelerating leaf senescence. There is extensive evidence of the effects of ambient ozone concentrations in reducing crop yields in western Europe and North America, but the evidence of the impacts of ozone on crop yield in other regions is limited. In Pakistan, studies by Wahid *et al.* (1995a, b) demonstrated that filtering ambient air pollution at a site at the edge of the city of Lahore resulted in yield increases in local varieties of wheat (*Triticum aestivum*) and rice (*Oryza sativa*) of about 40%, at a site where sulphur dioxide (SO_2) concentrations are negligible but there are significant concentrations of nitrogen dioxide (NO_2) and ozone. Subsequent controlled fumigation studies with these varieties demonstrated that, whereas NO_2 at the concentrations found at the Lahore site had no effect on growth or yield, ozone at these concentrations had very substantial effects on local cultivars of both wheat and rice (Maggs & Ashmore 1998). Experiments with ozone protectant chemicals have also indicated that ozone can cause significant effects on the yield of *Lycopersicon esculentum* in and around New Delhi, on radish and turnip yields at a rural site in the Nile delta (Hassan *et al.* 1995), on yields of *Phaseolus vulgaris* in the Valley of Mexico (Ashmore & Marshall 1999; de Bauer 2003), and on soybean (*Glycine max*) in the Pakistan Punjab (Wahid et *al.* 2001). Although no direct evidence of adverse effects of ozone on crops in mainland China is available, recent data demonstrate that rural ozone levels are high enough to potentially affect yields of winter wheat (Chameides *et al.* 1999) and other crops (Zheng *et al.* 1998).

Figure 2 indicates locations around the world where there is well-documented evidence of visible injury or effects on yield, superimposed on modelled mean ozone concentrations for 1990, predicted using a global three-dimensional atmospheric chemistry model (Collins *et al.* 2000). How large is the effect of ozone on crop yields implied by these global ozone exposures? This requires combining spatial distributions of ozone exposure with appropriate relationships between ozone exposure and crop yield, and then placing an economic value on the estimated yield loss. In North America and Europe, exposure–yield relationships for annual crops have been derived from experimental studies, and used both to establish critical levels, or air quality standards, for significant effects on yield, and to assess economic impacts (Fuhrer, Skarby & Ashmore 1997; Mauzerall & Wang 2001). Evaluations of the national economic impact of ozone on crop yield have indicated values of the order of US\$2–4 billion in the United States (Adams *et al.* 1988; Murphy *et al.* 1999) and of 4 billion Euros in Europe (Holland *et al.* 2002), although there are many assumptions involved in these estimates. On a global scale, Chameides *et al.* (1994) used economic projections which suggested that global NOx emissions would increase from 110 kT d^{-1} in 1985 to between 150 and 180 kT d^{-1} in 2025. Their model predicted that the proportion of the world's cereal crop exposed to ozone levels above an assumed threshold for significant (i.e. > 10%) effects on yield would increase from 9 to 35% in 1985 to 30–75% in 2025. Much of this increased area of cereal production at risk was in Asia. For China, Aunan, Bernsten & Seip (2000) estimated that projected increases in ozone precursors are likely to lead to significant national yield losses in wheat, soybean and maize (*Zea mays*) by 2020. More recently, Wang & Mauzerall (2004) also predicted large increases in yield losses caused by ozone in rice, wheat, maize and soybean by 2020 in East Asia, and suggested that China in particular was on the cusp of substantial reductions in grain production.

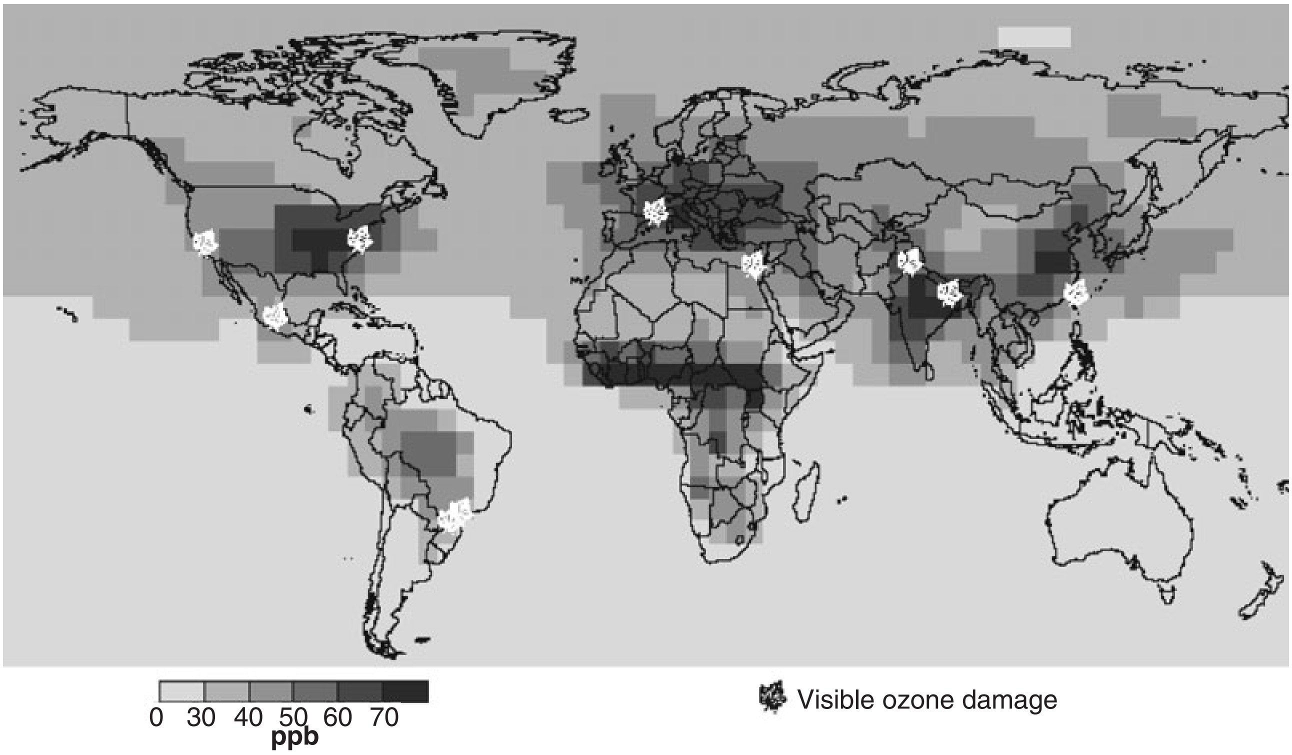

Figure 2. Global distribution of mean maximum growing season ozone concentrations based on 1990 emissions, using the global three-dimensional atmospheric chemistry model of Collins *et al*. (2000). The leaf symbols indicate regions where visible injury or yield reductions caused by ozone have been demonstrated. From Emberson *et al*. (2003).

However, it is important to recognize the many limitation of these estimates, which employ photochemical models with coarse temporal and spatial resolution to predict ozone exposures, take no account of climate and other modifying factors, and which use exposure–yield relationships derived from US or European cultivars, rather than from local varieties under local conditions. Most importantly, the use of exposure–yield relationships derived from experimental studies, that link yield to atmospheric concentrations rather than the flux of ozone to sites of damage in the plant, may lead to systematic errors in the evaluation of the size of the impacts on yield, and their spatial distribution.

In typical exposure-response experiments, ozone is added simultaneously in all treatments, i.e. under the same micrometeorological conditions. The ozone treatments over the experimental period are characterized by exposure indices, most commonly as the mean concentration during specific hours of the day (e.g. 7 h mean concentration; Adams *et al*. 1988) or the cumulative exposure above a threshold concentration of 40ppb during daylight hours (AOT40; Holland *et al.* 2002; Wang & Mauzerall 2004). However, these exposure-response relationships cannot reliably be used to compare the impacts of ozone in different locations, or in future years, because the different climatic conditions may lead to variable impacts of the same concentrations of ozone. This is significant because, in the field, the highest ozone concentrations tend to occur under meteorological conditions which limit the flux of ozone into the leaves, because of the high resistance to ozone flux across the atmospheric boundary layer to the vegetation, and because such concentrations often occur with high vapour pressure deficits, which lead to low values of stomatal conductance (Grunehage & Jager 2003). In ecosystems with summers associated with drought stress and large reductions in stomatal conductance, ozone exposure is very poorly correlated with measured or modelled ozone flux (Panek & Goldstein 2001; Panek, Kurpius & Goldstein 2002). It has also long been argued that differences in sensitivity of plant species can at least partly be explained by the different values of stomatal conductance (Reich 1987).

USE OF FLUX-BASED ASSESSMENTS

Over the past 5 years, there has been intensive debate in Europe about the possibility of replacing exposure indices, and in particular the AOT40 index (Fuhrer *et al*. 1997), by modelled cumulative flux or uptake, for regional risk assessment, as this could account to some extent for the influence of climatic and ontogenetic factors. The key questions are whether the use of flux provides an improved fit to experimental data, and whether it is possible to apply flux effectively in regional risk assessment. These questions have direct relevance to the methods use to assess the risk of ozone impacts in other parts of the world, and under different future climatic scenarios.

Analysis of experimental data for wheat (*Triticum aestivum*) collected over several seasons in southern Sweden, for which yield data were related to the ozone exposure

(AOT40) over the period of grain filling, showed that there was a wide variation in the slope of the relationships in different years. However, when they were related to the modelled absorbed dose of ozone through the stomata over the same period, five of the six experiments fell on a common line (Pleijel *et al*. 2000). This indicates the value of incorporating the effects of variable irradiance, temperature and vapour pressure deficit in modifying ozone uptake in the different years, in order to obtain a stronger relationship to yield of greater predictive value. Field data also support the use of the flux approach for trees. For example, thresholds for visible leaf injury to mature and young beech (*Fagus sylvatica*) trees at different sites were very different in terms of ozone exposure expressed as AOT40 (depending on age, location and season), but very similar in terms of modelled cumulative stomatal ozone flux (Baumgarten *et al*. 2000; Matyssek *et al*. 2004).

Relationships between ozone flux and yield have now been established for wheat (Danielsson, Gelang & Pleijel 2003; Pleijel *et al*. 2004) and potato (*Solanum tuberosum*) (Pleijel *et al*. 2002, 2004) using combined data from experiments across a range of soil and climatic conditions across Europe, for which the use of flux rather than external exposure (AOT40) produced a better fit to measured yield reductions. However, Karlsson *et al*. (2004) reported that, when combining experiments from several locations for tree species, modelled flux provided no better fit to experimental data on growth reductions than did the AOT40 exposure index. This may reflect greater uncertainty in parameterizing the underlying model of stomatal conductance, and in particular the assumption of a fixed maximum stomatal conductance. Uddling *et al*. (2004) showed that, by using the measured value of maximum stomatal conductance from different experiments on *Betula pendula* in Sweden, Finland and Switzerland, reductions in growth were related more closely to modelled flux than to AOT40 (Fig. 3).

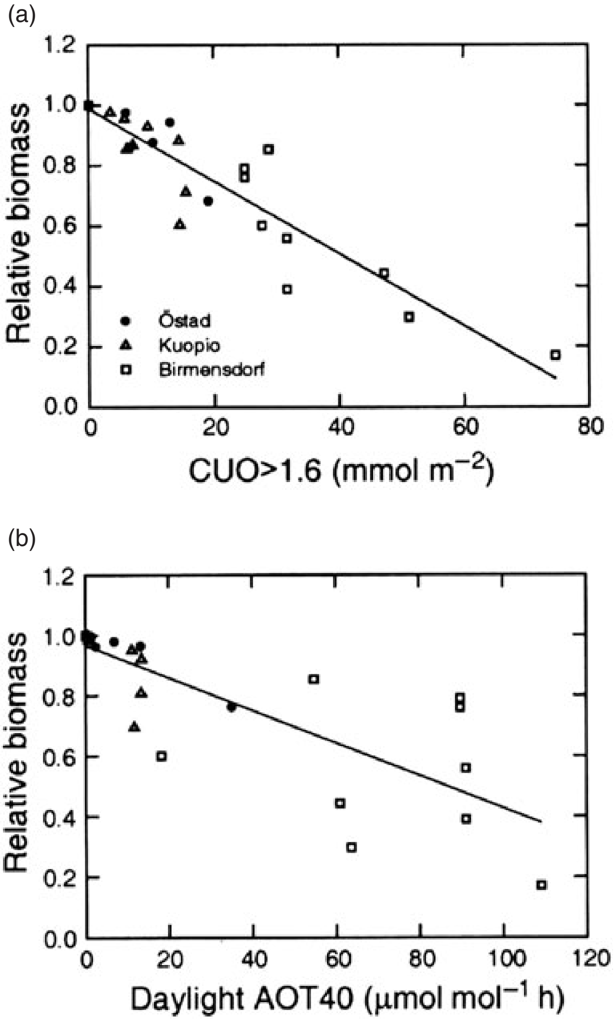

Figure 3. Relationships between biomass reduction relative to the control treatment in *Betula pendula* at three experimental sites and (a) cumulative ozone flux above a threshold of 1.6 nmol m^{-2} s^{-1} and (b) daylight AOT40. The different symbols indicate the different sites. From Uddling *et al*. (2004).

The flux indices proposed by Pleijel *et al*. (2004), Karlsson *et al*. (2004) and Uddling *et al*. (2004) all assume an instantaneous fixed threshold flux, below which there is no effect of ozone, which might be related to the capacity to detoxify incoming ozone. However, this threshold value is unlikely to be constant. For example, the birch data-set used by Uddling *et al*. (2004) contained an experimental study using 24 h exposure, and the outcome of their data analysis was dependent on assumptions about night-time flux. In this experiment, night-time exposure had a greater effect than daytime exposure, possibly because of reduced detoxification of ozone flux (Matyssek *et al*. 1995). Massman (2004) proposed a conceptual model of plant response linking estimates of ozone dose through the stomata to the capacity of defence mechanisms to detoxify the incoming ozone flux, which was assumed to be proportional to canopy assimilation rate. The approach of modelling flux above a critical flux has been used in leaf and whole plant models to successfully predict the effects of ozone on photosynthesis and on season-long growth (Martin *et al*. 2000, 2001), while more detailed models are available to describe the extent to which incoming ozone flux can be detoxified, for example, by reactions with ascorbate in the apoplast (Plochl *et al*. 2000). Busotti & Gerosa (2001) and Nali *et al*. (2004) have argued that the high ozone concentrations reported in forest areas of Mediterranean Europe represent a limited threat to native tree and shrub species. This is because of their high foliar concentrations of ozone defence compounds, and because summer peaks of ozone coincide with soil water deficits and stomatal closure, which may reduce the impact of ozone even on innately sensitive species such as *Pinus halepensis* (e.g. le Thiec & Manninen 2003).

The model of ozone response being dependent on stomatal flux and the capacity for detoxification of the incoming flux, has value in terms of an assessment of the impacts of changing patterns of ozone exposure. Figure 4 shows the relationship between hourly measurements of ozone concentration and modelled flux from studies with wheat (Danielsson *et al*. 2003). At maximal stomatal conductance, there is significant flux above the identified threshold value at concentrations above 24 ppb for wheat, that is, significantly below 40 ppb. This has important implications for evaluation of the significance of the changing patterns of global ozone exposure, since, based on this analysis, mean global background levels (Fig. 1) are already within the range at which significant flux to sites of damage in wheat may occur. At lower values of stomatal conductance, the threshold external ozone concentration corresponding to the critical flux is increased, whereas with a higher critical flux (detoxification capacity), the corresponding threshold ozone concentration is also increased.

Linking models of ozone flux and deposition to photochemical models of ozone formation can provide the tools to evaluate the effect of different emission control policies on ozone impacts based on modelled flux rather than exposure (Simpson *et al.* 2001). Such a model has now been developed for Europe, and has shown reasonable agreement with field measurements of ozone deposition (e.g. Tuovinen *et al.* 2004). There are significant differences between modelled spatial patterns of AOT40 and ozone flux over Europe that have important policy implications. For example, Emberson *et al.* (2000) showed that, whereas the highest AOT40 exposures were in central and southern Europe, high ozone fluxes to wheat and beech (*Fagus sylvatica*) were modelled in parts of northern and western Europe. Calculations of cumulative stomatal ozone dose over the growing season for wheat and beech for four different grid squares (in Sweden, UK, the Czech Republic and Spain), which experienced quite different AOT40 values, showed very little difference in the modelled cumulative stomatal dose, primarily because of the effects of differences in phenology and of modelled vapour pressure deficit.

These new risk assessment tools, based on ozone flux, rather than external concentration and exposure, now provide the basis for improved tools for regional policy assessment in Europe and North America. With appropriate parameterization, they will also provide a better assessment of potential impacts on yield in other parts of the world than the exposure–response relationships that have been used to date, because local climatic conditions can be incorporated. They also provide a stronger mechanistic basis for predictions of future impacts of changing ozone exposure patterns under a changing climate. However, much work is needed to improve the models for such applications. For example, an important limitation in regions with high ozone exposure is that altered stomatal responses to irradiance, VPD and Ci become apparent, leading to poor predictive power from models derived from observations at lower ozone exposure (Grulke *et al.* 2002). Similarly, Broadmeadow, Heath & Randle (1999) found that the reduced sensitivity of stomata to vapour pressure deficit at elevated CO_2 levels meant that the reduction in ozone flux in elevated CO_2 concentrations during ozone episodes may be less than assumed.

For trees, many experimental studies of ozone effects have been relatively short-term (5 years or less) and limited to seedlings or young saplings. Ozone exposure or flux–response relationships from such studies are unlikely to provide good predictions of the effects of ozone on mature trees. Samuelson & Kelly (2001) identified the use of potted seedlings in some experimental studies as an issue, because these, especially for angiosperms, tended to show lower values of stomatal conductance, probably because of restricted root growth, and hence limited soil water availability. Both Samuelson & Kelly (2001) and Kolb & Matyssek (2001) concluded that stomatal conductance, and hence ozone flux, is lower in sun leaves of mature trees than in leaves of soil-grown young trees, and has a different diurnal profile, both

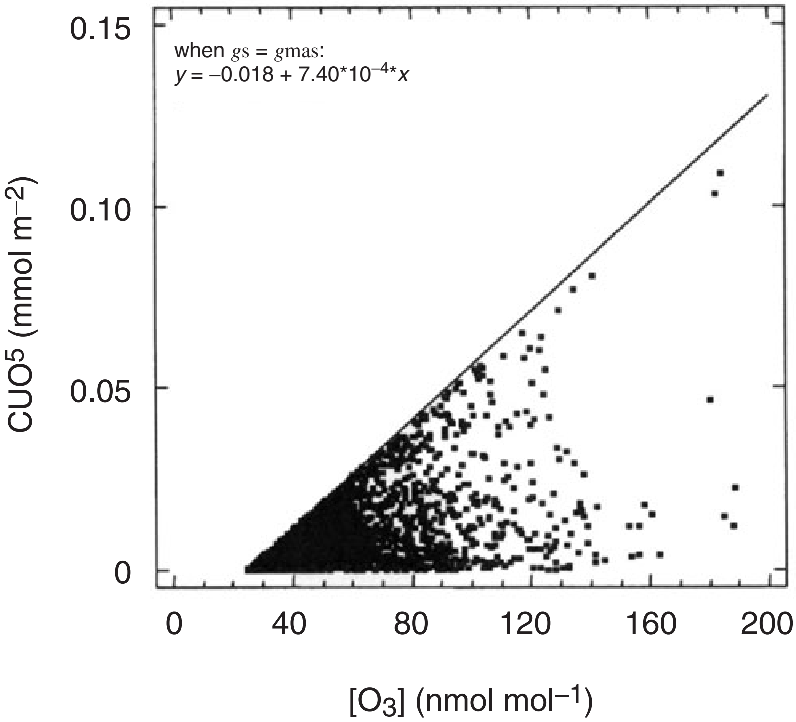

Figure 4. Relationship between hourly mean ozone concentration ([O_3] nmol mol^{-1}) and modelled cumulative hourly ozone uptake above a threshold flux of 5 nmol m^{-2} s^{-1} for wheat (*Triticum aestivum*). The solid diagonal line represents the relationship between the two variables when stomatal conductance is at the maximum value assumed in the model for this species; that is, it represent the highest possible cumulative uptake of ozone above the threshold (CUO^5) for a given ozone concentration. From Danielsson *et al.* 2003.

because of anatomical differences and because of the greater resistance to water transport in mature trees.

Kolb & Matyssek (2001) also hypothesized that the capacity for leaf defence and repair processes would be lower in leaves of mature trees because of lower rates of photosynthesis and higher respiratory rates. This is supported by the data of Fredericksen *et al*. (1996) for *Prunus serotina*, and the results of Wieser *et al*. (2002), who compared the response of *Picea abies* trees of different ages to cumulative ozone uptake, rather than external ozone concentration, and showed much greater sensitivity of young trees, which they related to a greater specific leaf area and a lower antioxidant capacity of the needles. It is also relevant to the observation that the impact of ozone is greater in the lower canopy and in shade-grown leaves than in the upper canopy, despite the lower ozone flux (Tjoelker *et al*. 1995; Fredericksen *et al*. 1996). Recent work by Wei *et al*. (2004) showed that leaves exposed to intermittent light flecks are more sensitive again than leaves grown under low light. This was associated with higher ratios between ozone uptake and net photosynthesis under both shade and intermittent light flecks, and hence a reduced capacity for defence and repair.

Variation in stomatal flux may also be associated with interspecific variation in sensitivity to ozone. Franzaring, Dueck & Tonneijck (1999) suggested that ozone sensitivity in wild plants was associated with particular ecological growth strategies, with fast growing competitive ruderal species tending to be more sensitive than stress tolerators. There are reports of weak associations between ozone sensitivity and higher growth rate or stomatal conductance in some studies (e.g. Reiling & Davison 1992; Bungener *et al*. 1999; Power & Ashmore 2002) but not in others (e.g. Pleijel & Danielsson 1997; Gimeno *et al*. 2004a). Van Oijen *et al*. (2004) have recently argued, based on a model of spring wheat responses to ozone, that a focus on specific parameters that are related to a combination of growth strategy and strategy of response to ozone might be more informative; on the basis of their model, light use efficiency, the fraction of assimilates used for leaf growth and maintenance, and the rates of detoxification and repair were identified as critical parameters. They demonstrated that a high growth rate can only be combined with ozone tolerance if there are high rates of detoxification, because of the high metabolic costs of repair.

IMPORTANCE OF CARBON ALLOCATION

Flux-response models do not specifically consider the secondary effects of the modelled impacts at the initial site of damage in the leaf, as mediated, for example, by changes in resource allocation within the plant. Figure 5 (from Fuhrer & Booker 2003) links the flux of ozone and the role of repair mechanisms and detoxification to changes in carbon allocation, either directly or indirectly, through its impacts on photosynthesis. The mechanisms underlying these effects, and their significance in determining how ozone causes reductions in agricultural yields, impacts on forest growth and vitality, and changes in the fitness of wild species, need further consideration. Translocation patterns to, and hence the growth rate of, different plant organs may depend as much on sink activities as on source strength and hence the impacts of ozone may depend on partitioning priorities at the time of exposure. Sellden & Pleijel (1995) suggested that the lower sensitivity to ozone of barley yield, compared with wheat yield, is due primarily to the larger potential surplus of carbohydrate for grain filling in barley, which means that grain yield is less sensitive to reductions in photosynthetic rate.

There is evidence from several species that ozone can have a direct effect on phloem loading. Grantz (2003) has argued, based on recent experimental evidence (Grantz & Farrar 1999; Grantz & Yang 2000) in Pima cotton (*Gossypium barbadense*), that ozone effects in reducing photosynthetic rate and stomatal conductance are secondary effects due to reduced phloem loading, through feedback inhibition and increased hydraulic resistance, respectively. Short-term ozone exposures reduced carbon efflux from the leaves of Pima cotton more than carbon assimilation, and the total carbon efflux to the roots was reduced by amounts

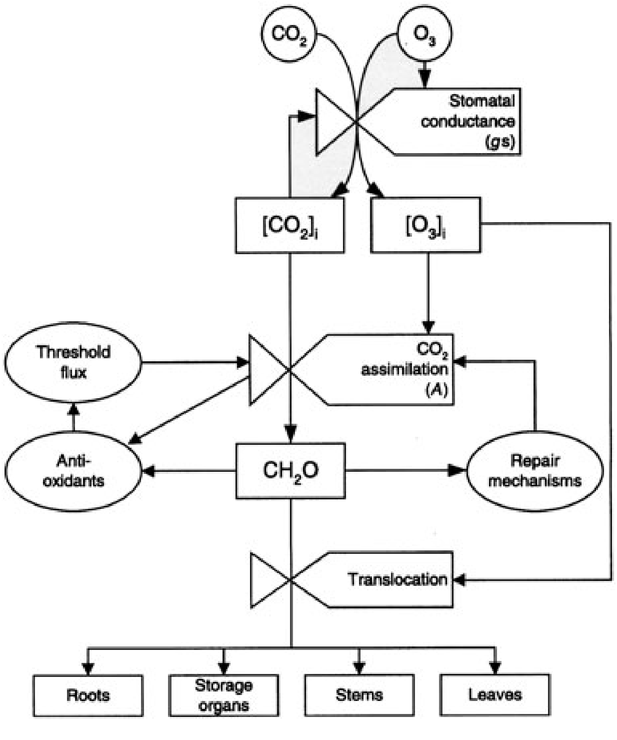

Figure 5. Conceptual model of the effects of CO_2 and O_3 on carbon assimilation and allocation, including links to detoxification and repair. CO_2 and O_3 enter through the stomata, and both may influence stomatal conductance and hence flux of the two gases into the leaf. Ozone may reduce the rate of CO_2 assimilation, and the availability of carbohydrates (CH_2O), which is influenced by CO_2 and O_3 concentrations, may alter both the capacity to repair ozone injury, and the supply of antioxidants, which influences the threshold flux above which ozone may cause injury. Translocation and allocation of carbon to different organs may be affected both by the availability of carbohydrates and by direct effects of ozone. From Fuhrer & Booker (2003).

that were very comparable to the effects of ozone on carbon efflux from the leaves (Grantz 2003). A key argument for this hypothesis is that, as has been reported in other species, soluble sugars in Pima cotton leaves increased under ozone stress at the same time as translocation declined. However, evidence from other species is consistent with the primary mechanism of reduced yield being reduced carbon assimilation. For example, from a meta-analysis of data on ozone impacts in soybean (*Glycine max*), Morgan, Ainsworth & Long (2003) argued that the cumulative data strongly suggested that effects on yield were associated with effects in reducing photosynthesis rates, rather than the latter being an indirect effect of impaired translocation. This was because foliar levels of non-structural carbohydrates decreased in ozone on average to a greater extent than did rates of photosynthesis. Nevertheless, to assess and model the impacts of ozone on the assumption that they are linked to primary effects on carbon assimilation may omit important processes that have different relationships to ozone exposure and flux.

The significance of the balance between source activity, sink activity and translocation clearly means that the timing of an ozone episode is an important factor, for determinate species in particular. Younglove *et al*. (1994) reported that exposure of several bean species to ozone during pod filling has a greater effect than exposure during earlier growth stages, while in *Lycopersicon esculentum* the period between flowering and fruit set was most sensitive to ozone. The development of flowers and fruits may itself influence sensitivity to ozone. Studies with deflowered plants of *Phaseolus vulgaris* by Tingey *et al*. (2002) showed an effect of pod development in increasing foliar ozone injury, which the authors suggested was related to the greater export of carbohydrates to the pods and reduced energy available for repair of ozone injury. Drogoudi & Ashmore (2001) reported that removal of fruit influenced the effects of ozone on the pattern of assimilate allocation in *Fragaria* × *ananassa*, with more carbon being retained in the petiole of the source leaf.

In wheat, the period between anthesis and grain filling is the most sensitive in terms of yield loss (e.g. Pleijel *et al*. 1998), and the key effect of ozone is an acceleration of leaf ageing, particularly of the flag leaf. For example, Pleijel *et al*. (1997) showed a strong positive association between the effect of ozone on the number of days with a green flag leaf and its effect on grain yield. Mckee & Long (2001) used plant growth regulators to demonstrate that effects of ozone on leaf development and carbon allocation were more important than direct effects of ozone on carbon assimilation in determining impacts on wheat yield. The ability to respond to increased leaf senescence by producing new leaves may be an important factor in indeterminate crops; Piikki, Sellden & Pleijel (2004) found that the leaf sensitivity of two potato cultivars was similar, but that an early season, more determinate, cultivar that produced few new leaves after flowering was more sensitive in terms of yield than a late season indeterminate cultivar. Kolb & Matyssek (2001) identified a switch from an indeterminate to a determinate growth pattern in more mature trees as an important factor in the greater sensitivity to the same ozone dose of mature trees compared to young trees. They argued that plants with a more determinate growth habit will tend to respond to ozone exposure by reducing carbon allocation to root growth and to defence against other stresses, in order to maintain the older leaves or to support new leaf flushes.

These dynamic interactions between plant development, carbon allocation and ozone exposure are important in understanding future impacts of ozone, as the seasonal patterns of ozone exposure in the northern hemisphere may change, with fewer summer peaks and earlier exposure at the stage of germination and establishment (Coyle *et al*. 2003). At the same time, rising temperatures and CO_2 concentrations will change the timing of phenological development, carbon dynamics, and growth rates. Early season exposure may be particularly important in tree species; Mansfield, Paul & de Silva (2001) showed that early season exposure to ozone had a greater effect in beech (*Fagus sylvatica*), due to an increased sensitivity of leaves in the first few weeks. Early season exposure to ozone for 6 weeks has been shown to influence the competition between herbaceous species over the remainder of the growing season (Fuhrer *et al*. 2003). The effect of warming, particular at high latitudes, may be to lead to an earlier bud burst, but possibly also to an increased risk of damage caused by early spring frosts; these may be associated with higher ozone exposures early in the growing season. Prozherina *et al*. (2003), working with *Betula pendula*, showed complex interactions between ozone, budburst and frost, which depended on genotype, and suggested that ozone may reduce or delay compensatory leaf production after frost damage.

In terms of ozone effects on wild species with different ecological strategies, the traits of relevance are those that relate most directly to ecological fitness, rather than visible symptoms or vegetative growth (Davison & Barnes 1998). Seed output is of greatest ecological significance for ruderal species, whereas for competitor species, the capacity to alter resource allocation in response to competitive pressure is important, and the critical response for perennial stress-tolerant species may be the extent to which ozone alters sensitivity to specific stress factors. Hence, effects of ozone on resource allocation may be more important than those on photosynthetic capacity for many wild species. The available data indicate that there is considerable variation between species in effects on resource allocation. Bergmann, Bender & Weigel (1995) showed that, of 17 species, ozone caused comparable reductions in both vegetative and reproductive biomass in 12 species, but that in two species resources were switched to reproductive growth, and in three species, resources were switched to vegetative growth, in ozone. Other studies have shown delayed onset of flowering and/or reduced flower numbers in wild species (Bergweiler & Manning 1999; Franzaring *et al*. 2000; Gimeno *et al*. 2004b), although Power & Ashmore (2002) reported an acceleration of bud production in two wetland species. In terms of effects on root growth and morphology, Warwick & Taylor (1995) showed that the below-ground effects of ozone on different calcareous grassland species could be very different from those on above-ground growth, and that species differed in the nature of the root response. Batty & Ashmore (2003) showed that, among wetland species, threshold ozone concentrations for effects on root biomass were consistently lower than those for effects on shoot biomass.

For forests and other semi-natural ecosystems, the effects of ozone on resource allocation need to be considered over a longer time frame. Furthermore, nutrient and water supply may be critical factors for forest vitality and growth, or for survival of wild herbaceous species, while small changes in crown or root development can eventually lead to changes in competitive balance between or within species. Reduced allocation of carbon to root growth has been demonstrated in experiments on young trees of several species including *Betula pendula* (Oksanen & Rousi 2001; Karlsson *et al*. 2003b). In certain species, loss of older leaves and reductions in photosynthetic rate can be compensated by increased production of new leaves with higher photosynthetic rates (e.g. Woodbury, Laurence & Hudler 1994), but this may be at the expense of carbon partitioning to the root. Martin *et al*. (2001) simulated large reductions in root growth, consistent with those found in experiments, in *Populus tremuloides*, due to accelerated senescence of the older leaves of the lower canopy that export most of their assimilate to the roots. There are limited data on root responses to ozone in mature trees in the field, although Grulke *et al*. (1998) reported much lower root biomass of *Pinus ponderosa* in the spring at sites with higher ozone exposures. Hence, understanding and modelling of changes in carbon allocation in response to ozone exposure are crucial to predicting its long-term impacts in the context of global change, including those on the capacity of species to adapt to changing nutrient and water availability.

IMPACTS ON REPRODUCTIVE ORGANS AND PLANT CHEMISTRY

There are other important effects of ozone that are not considered in the conceptual model of Fig. 5. Firstly, although it is widely assumed that effects of ozone on reproductive organs are mediated through reduced carbon allocation, ozone may also have direct effects on reproductive structures. Black *et al*. (2000) identified studies that show direct effects of ozone on pollen germination and tube growth, fertilization, and the abcission or abortion of flowers, pods and individual ovules or seeds (e.g. Bosac *et al*. 1994; Stewart *et al*. 1996; Schoene, Franz & Masuch 2004). These direct effects may be important to consider in assessing impacts of ozone in the context of global change. Mckee, Bullimore & Long (1997) found that elevated CO_2 prevented any adverse effect of ozone on vegetative growth of winter wheat, but that there was an additional effect of ozone on grain yield on which elevated CO_2 appeared to have no effect, which they proposed was related to direct effects of ozone on the grain itself.

Secondly, the effects of ozone on crop quality, although poorly researched, may also be significant. Soja *et al*. (2004) showed that juice quality in grape (*Vitis vinifera*) was more sensitive to ozone than grape yield, and that, while the impacts of ozone on yield were strongly related to ozone exposures in the 2 years prior to harvest, juice quality was best related to exposure in the current and previous year. Ollernshaw, Lyons & Barnes (1999) showed a significant reduction in both seed yield and the oil content of harvested seeds of oil seed rape (*Brassica napus*); since contract price for this crop in the UK is based on oil content, this effect of ozone would be an additional economic loss to the producer. The CHIP study of ozone impacts on potato at seven different sites across Europe reported that effects on crop quality were as important as those on crop yield (Craigon *et al*. 2002; Vorne *et al*. 2002; Vandermeiren 2005). Pooling the results across the sites, ozone caused a 8% reduction in yield of marketable tubers, but this was offset by a 28% reduction in the reducing sugar content and a 15% increase in ascorbate content, both of which will have a positive effect on quality. The quality of three North American warm-season forage species has been reported to be decreased by ozone, in the absence of significant effects on growth, with nutritional and economic implications for their use by ruminant herbivores (Muntifering *et al*. 2000; Powell *et al*. 2003). Studies of managed pastures in both Europe (e.g. Fuhrer *et al*. 1994) and North America (e.g. Montes, Blum & Heagle 1982) have demonstrated that increased ozone exposure reduces clover biomass and hence forage quality in grass-clover swards, and that regular cutting enhances this process, probably because of the reduced capacity for re-growth of clover exposed to ozone.

Thirdly, changes in foliar chemistry and surface characteristics caused by ozone may have a range of important secondary effects, for example on the incidence of viral and fungal diseases and the impacts of insect pests (Fluckiger, Braun & Hiltbrunner 2002). Most experimental studies have grown crops under conditions which prevent the occurrence of pests and diseases, while many commercial fungicides and pesticides have been shown to provide significant protection against ozone injury (e.g. Taylor & Rich 1973), and this is an important factor both in interpreting experimental studies and in assessing the extent of damage to crops in the field. Insect outbreaks may be more common in a warmer world (Bale 2002), and it was recognized over 30 years ago that ozone-damaged trees in the San Bernadino mountains were more frequently infested by bark beetles, possibly due to changes in resin flow rate and exudation pressure (Stark & Cobb 1969). Dahsten, Rowney & Kickert (1997) reported higher fecundity in western pine beetles affecting oxidant-damaged trees compared with healthy ponderosa pine, and also found more beetle predators and parasitoids on healthy trees.

Most studies have related changes in insect performance to changes in foliar concentrations of nitrogen, carbohydrates and phenolics. For example, the positive effect of ozone on the performance of forest tent caterpillars (*Malacosoma disstria*) feeding on *Populus tremuloides* was found by Kopper & Lindroth (2003) to be associated with both higher early season nitrogen concentrations and lower concentrations of phenolic glycosides. However, atmospheric emissions and reactions may also be significant. There is evidence that ozone, unlike SO_2 and NO_2, can damage the searching efficiency of parasitoids and the number of hosts parasitized, possibly because of interference with olfactory signals (Fig. 6; Gate, McNeill & Ashmore 1995). Arndt, Lorenz & Schachner (1996) demonstrated that reaction between ozone and pheromone extracts reduced their biological activity through chemical breakdown, although the significance of this in the field remains uncertain. Vuorinen, Nerg & Holopainen (2004) studied the effect of ozone on signalling in a tri-trophic plant/spider mite/predatory mite system, and showed that, although ozone induced similar volatiles to spider mite infestation, predatory mites could distinguish the two through olfactory cues; however, the ability of predatory mites to distinguish spider mite and non-spider mite-infested plants appeared to be weakened in the presence of ozone. Holton *et al.* (2003) reported that tree–herbivore–parasitoid interactions could be modified by both ozone and elevated CO_2 concentrations in ways that were dependent on genotype. How these bi- and tri-trophic interactions will be altered by rising ozone exposures, when other elements of global change may be causing changes in foliar chemistry, emissions of volatiles, and insect population dynamics, is very uncertain.

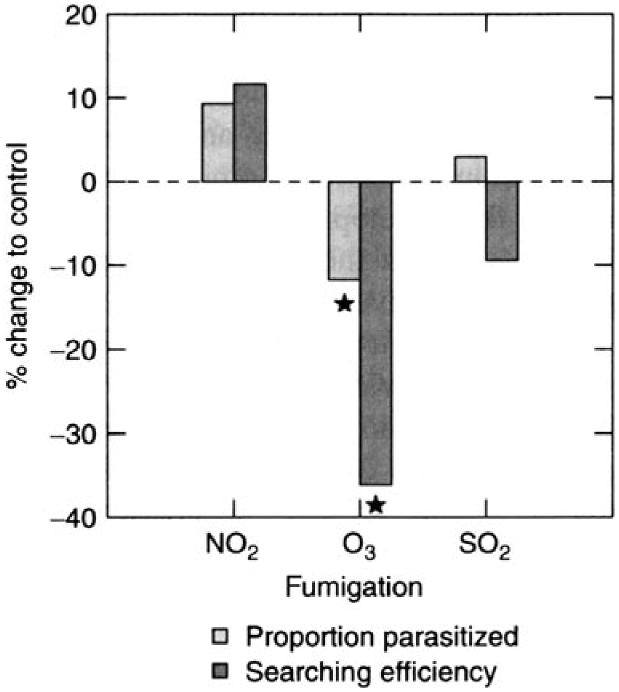

Figure 6. The effects of three air pollutants on the parasitism of host larvae of *Drosophila sabobscura* by the braconid parasitoid *Asobara talida*. The proportion of *Drosophila* larvae parasitized by *Asobara tabita* (light columns) and the searching efficiency of the parasitiod (dark columns) are expressed relative to a filtered air control treatment. The results show the effects of exposure of the host/parasitoid system to 100 nL l^{-1} of NO_2, SO_2 or O_3. Both parameters are significantly influenced by O_3 ($P < 0.05$), but not by the other two gases. From Gate *et al.* (1995), as modified by Fluckiger *et al.* (2002).

LONG-TERM ECOSYSTEM EFFECTS

The long-terms effects of ozone on individual perennial species or communities over several years of exposure remain uncertain. Although studies in grasslands have suggested a cumulative effect on clover biomass over several years (e.g. Montes *et al.* 1982), studies of wet grassland mesocosms (Tonneijck *et al.* 2004), grassland species (Bungener *et al.* 1999) and early successional forest communities (Barbo *et al.* 1998) suggest that the ozone sensitivity of perennial plants is greater in the first year than in subsequent years of exposure, possibly because of physiological or morphological acclimation processes. Several mechanisms for carry-over effects in trees have been identified, including impaired bud formation leading to reduced early growth of foliage in the next season in *Betula pendula* trees (Oksanen 2003), and reduced root carbohydrate content and new root growth in the spring in *Pinus ponderosa*, following a season of ozone exposure (e.g. Andersen *et al.* 1997).

Natural selection may operate to favour more ozone-tolerant genotypes as ozone exposures increase. Differences in ozone responses between populations from different locations are well established (e.g. Danielsson *et al.* 1999; Manninen *et al.* 2003; Bassin *et al.* 2004), but few of these studies have demonstrated that these are due to natural selection of ozone tolerance, except those with *Populus tremuloides* (Berrang, Larnosky & Bennett 1989) and *Plantago major* (Davison & Reiling 1995; Lyons, Barnes & Davison 1997). Other studies have failed to relate intraspecific variation in sensitivity to spatial variation in ozone exposure; for example, Lee *et al.* (1999) found large differences in ozone sensitivity of *Prunus serotina* clones which were unrelated to their geographical origin. Davison *et al.* (2003) investigated the cause of small-scale variation in injury symptoms shown by *Rudbeckia laciniata* in the Great Smoky Mountains. Populations of these plants were related to a small number of genets, but microclimatic factors were found to be more significant as factors influencing the degree of injury than genetic differences.

The long-term effects of ozone on biogeochemical cycling are poorly understood. There is little evidence that ozone affects rates of litter decomposition, although it is known to affect the secondary chemistry of leaves (Scherzer, Rebbeck & Boerner 1998; Kainulainen, Holopainen & Holopainen 2003). For example, Saleem *et al.* (2001) reported increased concentrations of leaf phenolics at the expense of impaired growth and increased leaf senescence in *Betula pendula*. Kim, Chappelka & Miller-Goodman (1998) reported that ozone caused reduced rates of decomposition, due to changes in substrate quality and soil microbial activity, and Islam, Mulchi & Ali (2000) also reported that ozone decreased microbial biomass. Olszyk *et al.* 2001) hypothesized that elevated ozone concentrations could influence below-ground foodweb biota, and C and N cycling, through changes in litter chemistry, root chemistry and root exudates. A 2-year mesocosm study showed no effect above ground on *Pinus ponderosa*, but a significant reduction in root N content, and evidence of reduced rates of N fixation in the litter. Loranger, Pregitzer & King (2004) reported that 4 years of ozone exposure decreased the abundance of soil Acari under tree stands, which they proposed was associated with declining litter quality.

Furthermore, responses to ozone may be modified by nutrient availability. Nutrient-limited *Plantago major* plants showed a greater reduction in seed production when exposed to ozone than did well-fertilized plants (Whitfield, Davison & Ashenden 1998), but, in contrast, in young *Betula pendula* trees, low nutrition enhanced the antioxidative defence capacity and delayed leaf loss under ozone stress (Maurer *et al*. 1997). Maurer & Matyssek (1997) suggested that nutrition may modify the nature of acclimation responses to ozone in this species; under high nutrient supply, leaf turnover is increased, but under low nutrient supply, there is increased investment in leaf defence and repair processes; both acclimation responses may lead to decreased carbon allocation to the roots. Ozone can also modify competition for nutrients; Andersen *et al*. (2001) reported that the presence of the grass *Elymus glaucus* increased the impact of ozone exposure on *Pinus ponderosa* seedlings. Ozone caused an increased needle N content in *Pinus ponderosa* without the grass, but a decreased needle N content with it, suggesting that the presence of *Elymus glaucus* reduced the capacity of the seedlings to take up or retain nitrogen in the presence of ozone.

A limited number of field studies have identified ozone as a factor associated with declines in forest growth over periods of decades both in areas of high ozone exposure (Peterson *et al*. 1995; de Bauer 2003) and in areas with lower ozone exposure, where it is difficult to separate effects of ozone from those of other factors, such as drought, temperature and insect outbreaks (Wager & Baker 2003: Dittmar, Zech & Elling 2003). Interactions between ozone and other stress factors, such as soil moisture availability, may be an important factor. Mclaughlin & Downing (1995) made short-term measurements of stem growth of *Pinus taeda* in the eastern United States, using a sensitive dendrometer, over a period of 5 years, and related these to records of weekly variations in ozone concentrations, climate and soil moisture stress. The results showed that the strongest predictor of short-term radial growth was the interaction between ozone and soil moisture, with the short-term ozone effect being greater in a moist year than a dry year. Ollinger, Aber & Reich (1997) used a canopy model, parameterized with experimental data on ozone effects on stomatal conductance and photosynthetic rate, to predict the impacts of ozone on the growth of hardwood forests. They found that predicted effects of ozone on wood production and net primary productivity at 64 sites in the north-eastern US were strongly modified by soil water-holding capacity, and that the results were sensitive to model assumptions about the interactions between ozone exposure, stomatal function and water stress. Forest models have also been used to assess potential effects of regional climatic differences in modifying ozone impacts. Yun, Park & Laurence (2001) compared predicted growth of *Populus tremuloides* in New York State and a location in Korea, where ozone levels have increased over the last decade, by parameterizing a growth model using US experimental data and then running it with local environmental data. Under Korean conditions, absolute growth rate and assimilated carbon was higher, and carbon allocation patterns changed, but the trees were predicted to be more sensitive to ozone.

The effects of ozone in modifying interspecific competition are uncertain. Studies in which artificial mixtures of herbaceous species have been exposed to ozone indicate that the performance of the more sensitive species tends to be reduced further by ozone in competition compared with monoculture (Ashmore & Ainsworth 1995; Davison & Barnes 1998; Fuhrer *et al*. 2003). However, the empirical evidence from the few studies which have examined the effects of ozone on intact communities suggest a more complex situation. Thus, Evans & Ashmore (1992) found that the effects of filtering ambient air pollution on an acid grassland community were the opposite of those predicted from the responses of the individual species, with ozone-sensitive forbs showing a greater cover in the treatment with higher ozone exposures. They hypothesized that this was due to these species responding to changes in the cover of the dominant grass species, rather than directly to ozone. Barbo *et al*. (1998) found that ozone caused a significant decrease in species richness, species diversity and species evenness of an early succession forest community, but that effects on individual species may be more difficult to predict. Thus, blackberry (*Rubus cuneifolius*) increased in cover in the highest ozone treatment, despite its known ozone sensitivity and despite showing clear visible symptoms of damage. Hence altered levels of competitive stress under ozone may cause secondary effects on community composition which cannot readily be predicted from the known sensitivity of individual species.

The importance of several of the factors discussed above, operating together over decades, is well illustrated in an area, the San Bernadino mountains, where the impacts of ozone stress on forest community composition have been intensively studied (Miller & McBride 1999). The dominant species of these mixed-conifer forests historically were ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*), due to their tolerance of the frequent wildfires, but these are also the most sensitive species to ozone. Both species have shown severe foliar injury and reduced needle longevity, associated with reduced radial growth, and are more susceptible to attack by bark beetles, outbreaks of which are associated with drought years. Regeneration in these forests is now greater for other tree species which are more resistant to ozone, and also are favoured by current fire exclusion as they are more fire-sensitive. Arbaugh *et al*. (2003) reported that long-term changes in species composition over 25 years were attributable to a complex mix of factors, including ozone exposure, nitrogen deposition, precipitation and management. The greatest change in species composition was associated with sites with high levels of pollution and water stress. Jones *et al*. (2004) presented evidence that the impacts on pines of greatly increased bark beetle activity associated with four consecutive drought years was enhanced in trees with visible ozone injury and at sites which experienced higher levels of nitrogen deposition.

Hence, the long-term effects of ozone on plant species composition and ecosystem function are uncertain and cannot be considered in isolation, since they depend on a number of other factors, including nutrient availability and cycling and water stress, that are important components of global change

CONCLUSIONS

It is vital, as argued by Ashmore & Bell (1991), that the predicted future changes in ozone concentrations, exposure patterns and global distribution are considered as an important component of global change. There are many ways in which the impacts of ozone on vegetation globally may be modified by changing CO_2 levels, climate, insect distributions, nutrient availability, etc. Furthermore, the changing global patterns of ozone may influence atmospheric concentrations of other radiatively active gases, through impacts on vegetation, for example by reducing above-ground productivity, and more speculatively, soil carbon storage (e.g. Loya *et al*. 2003) and methane emissions (e.g. Niemi *et al*. 2002).

The current global impacts of ozone are likely to be considerable. Patterns of global exposures to ozone are likely to change dramatically over the next 50 years and may act as a significant constraint on global food production and ecosystem function. The extent to which ozone exposures increase over this period is closely linked to the emission scenarios for energy production, transport, agriculture and industry, which form the basis for predictions of the impacts of climate change. Hence it is essential that evaluations of the impacts of different emission scenarios by the IPCC include a full assessment of the implications for ozone impacts on food production and ecosystem function.

However, we currently lack the experimental and field data outside North America and western Europe, and the risk assessment tools, to provide any more than a basic estimate of the likely global scale of the problem. Furthermore, our ability to predict the impact of potential changes in ozone exposure under different emission scenarios in the context of other factors associated with global change that will modify its impacts, is very limited. The development of flux-based models linked to effects on carbon assimilation and allocation offer a basis to improve the capacity for risk assessment, but there are a range of potential impacts of ozone, especially at the ecosystem level, for which the necessary mechanistic understanding does not exist to allow their inclusion in local or global risk assessments.

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