More harmful climate change impacts in polluted forests – A review

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Forests are facing significant pressures from climate change and air pollution. Air pollution is the main driver of the ongoing climate change. Current knowledge suggests that climate change may become more harmful to pollution-affected forests, although the magnitude of these feedbacks is still to be determined. At present, the air pollutants of most concern to forests are tropospheric ozone and nitrogen deposition. Both ozone and nitrogen affect biodiversity and increase forest susceptibility to drought, pest attacks, windstorms and fire. The impacts on forest ecosystems, however, have traditionally treated air pollution and climate change separately, although they are, in fact, cause and effect. The cause and effect relationship between pollutant inputs and ecological factors or ecosystem attributes requires substantial multidisciplinary research effort. The integrative effects of air pollution and climatic changes, in particular those caused by elevated ozone, altered nutrients, temperature, water availability, and elevated CO_2, will be key issues for future research. An important improvement in our understanding will be obtained by the combination of long-term multidisciplinary experiments with ecosystem-level monitoring, and integration of effects utilizing ecosystem modeling within a multiple-constraint framework. This paper reviews the current knowledge on the integrated climate change and air pollution impacts on global forests, and suggests mitigation strategies, adaptive forest management options, and how to close knowledge gaps for appropriate decisions in environmental policy.

Key words: Climate Change, Air pollution, Integrated approach, Knowledge gaps, Policy-making

Introduction

Combustion of fossil fuels, generating air pollution, is the main driver of the ongoing climate change, the complex of greenhouse gas-generated global changes in temperature, shifts in precipitation, and an increase in frequency, extremity, and intensity of storms. Many air pollutants and greenhouse gases have common sources, contribute to earth's radiative balance, interact in the atmosphere, and jointly affect ecosystems (Bytnerowicz *et al.*, 2007). Over the past 20 years, the focus of air pollution on forest science has moved from forest decline to a holistic framework of forest health, and from effects on forest production to impacts on all services provided by forest ecosystems, i.e., sustained biodiversity, soil protection, water balance and socio-economical benefits (Paoletti *et al.*, in press). Current knowledge suggests that climate change may exacerbate forests already affected by excessive pollution, although the magnitude of these feedbacks is still to be determined (Paoletti *et al.*, in press). Climate change is the defining environmental problem of the twenty first century. Temperature stabilization at or below 2°C above pre-industrial temperatures is considered the goal of climate change policy (Moore, 2009). The current Kyoto Protocol regulates only six gases: carbon dioxide, methane, nitrous oxide, hydrofluorocarbons, perfluorocarbons, and sulfur hexafluoride. These gases are all relatively long-lived and thus can be relatively easily compared with carbon dioxide. Additional warming comes from short-lived agents such as black carbon (a component of soot) and tropospheric ozone. Direct effects of black carbon on forests are negligible, while tropospheric ozone is a powerful phytotoxic pollutant.

This paper reviews the current knowledge on the integrated climate change and air pollution impacts on global forests, and suggests how to close knowledge gaps for appropriate decisions in environmental policy.

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Air pollutants affecting forest health

The air pollutants of most concern to forests are tropospheric ozone (O_3) and nitrogen deposition. Nitrogen oxides (NOx) are released into the atmosphere as a by-product of any combustion, where N in the air is oxidized to NO and in part to NO_2. NO is converted to NO_2 by photochemical reactions involving hydrocarbons. NO is also produced biologically by bacteria. NO_2 is also emitted from chemical factories, e.g. during the production of fertilizers. Fertilizer production, excessive N fertilization and animal farming are important sources of ammonia (NH_3). Release of NOx also results in nitric acid (HNO_3) deposition, and - at least locally - increases radiative forcing. NOx concentrations in many industrialized countries are expected to decrease, but rapid economic development has the potential to significantly increase emissions of N compounds in parts of Asia. Emissions of NO_2 and NH_3 decreased 32.6% and 27.3%, respectively, in the EU from 1980 to 2000 (Agren, 2003). In the US, NO_2 emission decreased 15% over about the same period, while NH_3 emission increased 3% (EPA, 2000). Increasing NH_3 emissions are also predicted for Asia, and will be seen mostly in China (Klimont *et al.*, 2001). Measurements of tropospheric NO_2 showed that the world's largest amount occurs over Beijing and the northeast China (Richter *et al.*, 2005). Some of these pollutants, such as NO_2, NH_3, HNO_3 or peroxyacetyl nitrate (PAN) can be toxic to plants at high ambient levels (Bytnerowicz *et al.*, 1998). These pollutants can be deposited in a dry form to forests, and together with the wet-deposited N, may significantly affect nutrient balance of forest stands (Aber *et al.*, 1989). Various negative effects of elevated N deposition have been described, including changes in species composition, reduced resistance to drought and insects, and increased susceptibility to catastrophic fires (Grulke *et al.*, 2009).

Tropospheric O_3 is an important phytotoxic air pollutant and a significant greenhouse gas (Bytnerowicz *et al.*, 2007). While O_3 is disappearing in the stratosphere, ground-level O_3 concentrations are increasing all over the world. Around 90% of total O_3 is in the stratosphere and just 10% is in the troposphere. Hence, the increase in tropospheric O_3 cannot compensate for the loss in stratospheric O_3. In addition, O_3 in the troposphere damages human and ecosystem health and amplifies the greenhouse effect. The formation of O_3 in the troposphere is the result of reactions between solar light and precursors, mainly NOx and volatile organic compounds (VOCs) as well as methane (CH_4) and carbon monoxide (CO). The overall reactions, however, are complex and non-linear (Stockwell *et al.*, 1997). VOCs include hydrocarbons and organic atmospheric trace gases other than carbon dioxide (CO_2) and monoxide. VOCs are generated from both man-made sources (anthropogenic) and natural sources (biogenic). Vegetation emits biogenic VOCs that include isoprenoids (isoprene and monoterpenes) as well as alkanes, alkenes, carbonyls, alcohols, esters, ethers, and acids. Isoprene is the most abundant hydrocarbon emitted by terrestrial vegetation (530 Tg C yr^{-1}), and may contribute to increase O_3 to +8–12 ppb in the mid-latitude land areas (Wang and Shallcross, 2000). Because of anthropogenic emissions of precursors, background O_3 levels have been rising since the first measurements in 1874 (~10 ppb, Marenco et al 1994). Annual average concentrations over the mid latitudes of the Northern Hemisphere currently range between 20 and 45 ppb, and are expected to be 42 to 84 ppb by the year 2100 (Vingarzan 2004). In the last decades, control strategies have limited the emission of precursors so that O_3 peaks have decreased in North America, Europe and Asia. However, background levels continue to increase (Midgley et al 2002; EEA, 2007). Trans-continental transport of O_3-enriched air masses has been demonstrated (Derwent *et al.*, 2004). Ozone concentrations in downwind rural and forested areas are usually higher than those in the city (Gregg *et al.*, 2003). Higher concentrations occur downwind for three reasons. First, O_3 is produced secondarily from primary sources (NOx) emitted in populated areas, which requires time and thus distance due to wind. Second, in urban areas, NOx from primary combustion sources titrates the O_3 that does occur there. Third, VOCs in green areas may contribute to the formation of O_3, since they are more reactive than anthropogenic hydrocarbons.

Synergetic effects of air pollution and climate change on forests

Atmospheric interactions

Even though tropospheric O_3 is a short-lived pollutant that tends to form local 'hotspots' of high concentrations, its radiative properties as a warming agent is global. IPCC estimates tropospheric O_3 radiative forcing at 0.39 W m^{-2} (Forster et al, 2007), thus ranking O_3 as the third most important anthropogenic greenhouse gas after CO_2 and CH_4. Ozone will also have an indirect effect on global warming

by reducing the capacity of vegetation to sequester C (Figure 1). This indirect radiative effect could increase the total radiative forcing due to O_3 over the period 1900–2100 by at least 70% (Sitch *et al*., 2007).

Projected changes in climate are likely to increase regional and local O_3 concentrations where emissions are high (Royal Society, 2008). An increase in the production of O_3 is influenced by increased temperature, increased sunlight, decreased humidity (all components of climate change), and the increase in long-range transport of pollutants (Figure 1). Interactions between climate and the terrestrial biosphere have an important effect on surface O_3 levels since vegetation is both a sink for O_3 and a source of VOCs, a precursor of O_3. Biogenic VOC emissions are sensitive to environmental factors such as temperature and light. One of the most important feedbacks between O_3 and climate is through temperature-increased emissions of O_3 precursors, including biogenic VOCs as well as NO from soils and CH_4 from wetlands (Royal Society, 2008). The expected increase in heat spells in the Northern Hemisphere will increase the frequency of high O_3 episodes. Ozone-induced reductions in stomatal conductance and transpiration imply reduced transfer of water to the atmosphere, decreasing humidity and potentially altering regional rainfall patterns in temperate and boreal forests (Wittig *et al*., 2009). Elevated levels of N deposition and saturation of ecosystems with N may lead to increased production of greenhouse gases, NO and N_2O (Fenn *et al*., 1996). Increasing concentrations of HNO_3 resulting from photochemical smog reactions and of NH_3 from intensive agricultural activities and use of catalytic converters, can lead to an increase of NH_4NO_3, a major component of fine particulate matter and regional haze. Regional haze may have pronounced effects on tropospheric transparency and the radiative energy balance (http://climate.eas.gatech.edu/yu/aerosol-land-intro.htm).

Carbon sequestration

Increased biomass accumulation in response to elevated CO_2 concentrations could dampen the future rates of increase in CO_2 rates and associated climate warming. However, it is not known whether CO_2-induced stimulation of plant growth and biomass accumulation will be sustained for a longer time considering N availability constrains (Reich *et al*., 2006) as well as deleterious effects of O_3 on C sequestration. In forests, N deposition together with higher temperatures, elevated CO_2 concentrations and intensified management will have strong effects on carbon (C) sequestration. Biomass production in most temperate and boreal forests is chronically restricted by a lack of N. Ecosystem CO_2 exchange could be expected to increase in response to increasing N deposition which would result in increased production of leaves and wood, including coarse roots (Oren *et al*., 2001). However, in ecosystems approaching N saturation, the effects of N may be less pronounced or even reversed leading to high N-leaching rates and mortality of some species (Magill *et al*., 2004). It should be kept in mind, however, that single-factor responses may be misleading because of various interactions between factors, in particular those between N and elevated O_3 exposure, and indirect effects such as increased N availability from temperature-induced decomposition (Hyvonen *et al*., 2007). This notion is also emphasized by Magnani *et al*. (2007, 2008): N deposition affects both gross primary production and ecosystem respiration. These two components of net ecosystem production seem to be affected by N deposition in opposite directions at the ecosystem level which is often missed when focusing on tree growth alone. These authors also stress a need for careful design of N fertilization experiments since they often overlook the role of canopy N uptake which

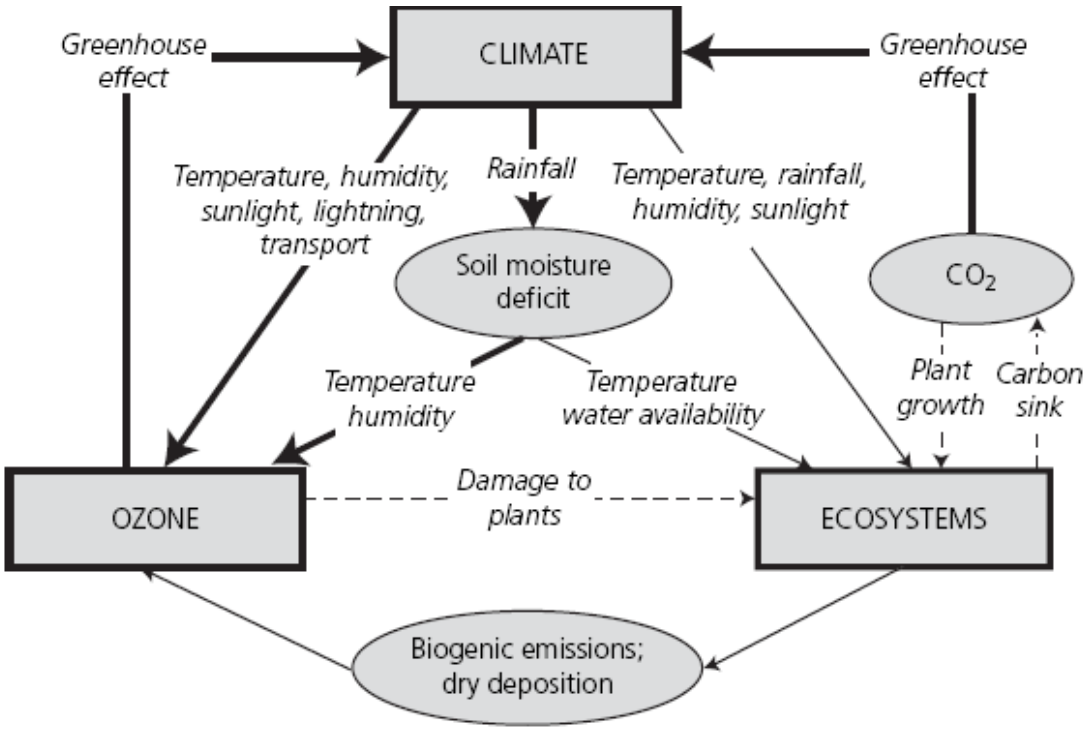

Figure 1. Schematic interactions between climate, ecosystems and tropospheric ozone. Thick lines denote processes that are well understood. Thin solid lines denote processes for which uncertainties exist. Dashed lines correspond to links that are emerging as important but not generally included in model projections.

Royal Society, 2008

enables plants to absorb a relevant fraction of incoming N without any competition from the soil microbes. Canopy uptake may amount to 70% of N deposition (Sievering, 1999). It is worth noting that in some Mediterranean ecosystems in California dry deposition of HNO_3, NH_3 and particulate NO_3^- and NH_4^+ may constitute up to 90% of total deposited N (Bytnerowicz and Fenn, 1996; Padgett *et al*., 1999), out of which up to 60% may be HNO_3 alone (Padgett *et al*., 2009).

Because O_3 reduces carbon assimilation (Wittig *et al*., 2007), there is a great concern about its impact on the reduced capacity of forest ecosystems to sequester C, although there are few long-term studies to fully assess this effect (Manning, 2005). A recent meta-analytic review of 263 peer-reviewed articles reporting O_3 impacts on northern hemisphere tree biomass showed that current ambient O_3 concentrations (40 ppb on average) significantly reduced the total biomass of trees by 7% compared with control trees in charcoal-filtered (CF) air, which approximate pre-industrial concentrations (Wittig *et al*., 2009). When elevated O_3 concentrations (64 ppb on average, close to the 68 ppb projected by 2050; Ehhalt *et al*., 2001) were examined, total biomass was reduced by 11% compared with trees at present ambient O_3, while 97 ppb (projected by the end of 2100) reduced total biomass by 17% relative to pre-industrial levels, which is a further 10% reduction relative to today. These results demonstrate that O_3 has been reducing the C-sink strength of northern hemisphere forests since the pre-industrial age and will further reduce it in future (Wittig *et al*., 2009).

These conclusions were based on controlled experiments with young trees. This kind of results cannot simply be translated to adult trees in the field (Kolb and Matyssek 2001), although negative correlations between stem growth and ambient O_3 exposure in mature trees in the field have been reported (Braun *et al*. 1999; Karlsson *et al*. 2006; McLaughlin *et al*., 2007). By comparing biomass reductions in aspen (*Populus tremuloides*) from the Aspen-FACE in Rhinelander (King *et al*., 2005) and in *Populus* species from the meta-analysis, similar values were obtained (-21% and -22%, respectively) although O_3 exposure was lower in the former than the latter (50 ppb and 60 ppb, respectively) (Wittig *et al*., 2009). As most of the studies in

the meta-analysis were short-term experiments in artificial chamber environments, this suggests a greater impact of O_3 when applied in open-air and is consistent with findings about soybean biomass in growth chambers (Morgan *et al*., 2003, 2005). Concern thus arises that the large losses projected across the chamber studies may be underestimates of what will occur in the real world and over longer, more realistic growth periods (Wittig *et al*., 2009). Further uncertainties arise from gaps in observations in the literature, that did not allow assessment of magnitude or significance of the interactions between O_3 and drought or O_3 and CO_2 (Wittig *et al*., 2009).

A maximum 31% loss in productivity of aspen in parts of its North American range between 2001 and 2003 was estimated to be caused by O_3 (Percy *et al*., 2007). Models, however, should include O_3 effects on both photosynthesis and plant avoidance/defence ability (Matyssek *et al*., 2007), as well as feedbacks and susceptibility resulting from reduced C allocation to belowground tissues (-15% of root-to-shoot ratio in Wittig *et al*., 2009). Ozone alters source–sink balance, resulting initially in C retention in shoots and decreased C allocation below ground to roots and mycorrhizae (Andersen 2003). Decreased allocation below ground alters C flux to soil, and soil processes. In parallel, above-ground allocation is affected. Compensatory growth of new leaves may occur, by using nutrient and C from declining leaves or reserve storage (Matyssek and Sandermann, 2003). Reduced branching, leaf size, and premature leaf loss may lower whole tree C sequestration from reduced photosynthetic surface area more than the decline in leaf photosynthesis itself (Matyssek, 2001). Trees that allocate less C to fine root system production are competitively disadvantaged for exploiting soil resources. Elevated O_3 and N deposition can alter root function and health by decreasing the degree of mycorrhizal colonization or altering community structure (Grulke *et al*., 2009). Ozone exposure increases lignification of aboveground tissues, decreases decomposability, and thus a more recalcitrant N pool develops (Treseder and Allen, 2000).

The complex range of effects on trees caused by O_3 also highlights the importance of understanding the combined effects of O_3 and other environmental factors, such as elevated CO_2. The predicted benefits of increased CO_2 concentrations on C storage may be offset at high O_3 concentrations. The total C incorporated into soil under aspen and aspen–birch components was reduced by about 50% over 4 years in the elevated O_3 + CO_2 FACE exposure compared with the elevated CO_2 treatment (Loya *et al*., 2003). Using the A2 scenario, Sitch *et al*. (2007) predicted a reduction in terrestrial C storage over the period 1900–2100 of 143 PgC, i.e. 17% of the C storage projected to occur due to increasing CO_2 concentrations over this period. Biogeochemical models suggest that O_3 may offset about 7% of the gains in productivity projected with increasing atmospheric CO_2 and N deposition (Ollinger *et al*., 2002; Felzer *et al*., 2004; Sitch *et al*., 2007). This type of large-scale model provides new insights into important global feedbacks, even though there are still significant uncertainties because parameterisation is based on a small number of long-term experiments which do not represent a range of global plant functional types, and neglect the combined effects of O_3, CO_2, N deposition, and climate (Royal Society, 2008). Additional uncertainties arise from O_3 effects on other greenhouse gases such as CH_4 (Fiore *et al*., 2002; Rinnan *et al*., 2003).

Ecological effects

At present, even at the highest concentrations, phytotoxic effects of NOx are very unlikely in forests of Europe and North America (Bytnerowicz *et al*., 1998). In the areas of rapidly increasing air pollution in China and other parts of Asia such negative effects should not be excluded. However, elevated levels of N compounds contribute to eutrophication. Examples are grasslands in the Netherland or coastal sage communities in southern California (Allen *et al*., 1998). Nitrogen deposition may have serious ecological effects on ecosystems (Fenn *et al*., 2005). While N is usually the growth-limiting nutrient in forest and semi-natural terrestrial ecosystems, chronic excess of N can lead to saturation manifested by increased leaching of inorganic N (generally nitrate). Increased leaching of nitrate enhances acidification of soils and surface waters and the risk of eutrophication of coastal marine areas and ground water quality. While in Europe and North America the critical loads for nutrient N are set generally between 5 and 15 kg N ha-1 y-1, such values were set much higher for sensitive Japanese evergreen broad-leaved species. Models suggest that N critical loads of 50 kg ha-1 y-1 have already been exceeded in parts of southern China (Kohno *et al*., 2005).

Increased atmospheric N deposition is well known to reduce plant diversity in natural and semi-natural ecosystems. Examples of such effects can be found in mixed conifer forest and coastal sage ecosystems in California (Allen *et al*., 1998; 2007). These effects occur also in many parts of the northern hemisphere and were studied mostly in Europe and North America. Based on the outputs from global chemistry transport models, Phoenix *et al*. (2006) predicted that by 2050 the biodiversity hotspots will double compared to mid 1990s, exacerbating the threat of N deposition to global floristic diversity.

The effects of elevated N deposition on disease have not been studied in detail, although N enrichment has been shown to increase fungal and bacterial diseases of foliage (Snoeijers *et al*., 2000). Nitrogen fertilization has also been shown to increase root rot of eucalyptus caused by *Phytophthora* species (Marks *et al*., 1973).

Although most of the O_3 effects research focus is on the C cycle, O_3 has a number of other effects on forest ecosystems that indirectly impact C sequestration but are not yet included in models. Ozone may weaken frost hardening and predispose trees to frost injury (Skärby *et al*., 1998; Ranford and Reiling, 2007). Ozone may affect plant/disease interactions (Manning and von Tiedemann, 1995). Ozone injury has been shown to predispose ponderosa pine to annosus root disease (*Heterobasidion annosum*; James *et al*. 1980) and black stain root rot disease (*Leptographium wageneri*; Fenn *et al*. 1989). Although long-term O_3 exposure reduce stomatal conductance, peaks affect stomatal control and may predispose trees to drought stress (Paoletti and Grulke, 2005). Mature deciduous trees from a mixed forest were shown to amplify diurnal water loss because of O_3-induced increases in sap-flow (McLaughlin *et al*., 2007). Ozone may alter tree leaf chemistry and insect herbivore performance (Percy *et al*., 2002; Valkama *et al*., 2007). In the San Bernardino Mountains, bark beetle activity and mortality of ponderosa and Jeffrey pine were positively related to O_3 injury and N deposition or experimentally amended N level (Stark *et al*., 1968; Eatough-Jones *et al*., 2004). Environmental factors that reduce stomatal aperture - such as drought and O_3 – and the root-to-shoot ratio – such as O_3 and N - consequently reduce both C acquisition in the short term (daily, cumulative) and nutrient flow in the transpirational stream to the foliage over the long term (months). When attacked, resin production provides both a physical and chemical impedance to bark beetle. Oleoresin pressure, related to the turgor potential of cells lining the resin ducts, forces pre-formed resin to the site of invasion. The moisture for cell turgor is derived from the transpirational stream, thus, if the tree is under O_3, N or drought stress, the resin pressure is reduced (Vité, 1961). Once mature bark beetles emerge from the galleries, they begin searching for a host. Interestingly, conifers under moderate drought stress produce jasmonate, a plant hormone that stimulates resin production (Zeneli *et al*., 2006). Dense stands of pine, overgrown from excess N deposition and historic land management practices, may produce ample signal (terpene production), which could alter nonolfactory aspects of short-range host selection behavior (Grulke *et al*., 2009). Warmer springs are anticipating the start of the second generation of bark beetles in the South-Eastern Alps (Faccoli, 2009), suggesting that climate change increases bark beetle pressure also by increasing the number of generations in a year.

Ozone also has strong biodiversity effects, e.g. by species-specific and individual-specific effects on resource acquisition and root/crown architecture, and thus space sequestration (Matyssek and Sandermann, 2003). In general, poor competitors have an added disadvantage in elevated O_3 (McDonald *et al*., 2002). Ambient O_3 can cause significant effects on photosynthesis of broadleaved species (-10%) and has less to no effect on conifers (Wittig *et al*., 2007), suggesting O_3 is giving conifers an advantage in mixed deciduous forest, which can lead to changes in community composition. Fast-growing pioneer species, such as birch, aspen and poplar, have been shown to be more O_3-sensitive than climax species such as beech and oak (Matyssek *et al*., in press). This has implications for future O_3 effects if climax species are replaced by fast growing plantations for agro-forestry and bio-fuel production (Royal Society, 2008). Ozone may also induce biodiversity changes by feedbacks on VOC emission (Lerdau, 2007). Biogenic VOCs can either ameliorate or aggravate O_3 pollution, depending on low or high concentrations of NOx (Lerdau, 2007). When plants emit isoprene into air with high NOx pollution, O_3 levels can increase. Recent advances, however, suggest that the damaging effects of O_3 are ameliorated by isoprene (Loreto and Fares, 2007, Velikova and Loreto, 2005). Isoprene-emitting species (e.g. oaks) will thus be better protected against O_3 damage than those that do not produce isoprene (such as maples, birches, or hickories). Most ecosystems consist of both VOC emitter and non-emitter species. Trees with VOC emissions will change the atmospheric composition in a way that causes more damage to non-emitters than to emitters. Over time, isoprene-producing taxa may become more abundant because of their greater resistance to O_3. This feedback could lead to changes in forest ecosystems, with decreased plant diversity and a cascade of effects on higher trophic levels and the atmosphere (Lerdau, 2007).

The global impacts of O_3 on biodiversity are difficult to predict because of gaps in knowledge. To date, O_3 responses of only a few dozen species in North America and Europe are known and little is known about the responses of tropical forests, grasslands and savannah. The areas of greatest risk are in eastern North America, the Alps and other Central European mountains, the northern half of South America, Central Africa and South-East Asia (Olson and Dinerstein, 2002). In total, O_3 decreases GPP more than 20% in 17 of the world priority-conservation ecoregions (G200), covering an area of 1.4 million km^2. Some of the hotspots at high risk from O_3 effects coincide with those at high risk from N deposition, including the forests of southeast Asia and southwest China and the cerrado of Brazil (Phoenix *et al*., 2006).

Mitigation strategies and adaptive forest management

Mitigating tropospheric O_3 means reducing emissions of precursor chemicals, particularly NOx and VOCs. Concentrating air pollution control on tropospheric O_3 is likely to yield significant cross-cutting benefits in terms of climate, human health, forests and agriculture. It is also likely to be highly cost-effective because much of the technology to control emissions already exists and has been deployed with effect in developed countries (Moore, 2009). Depending on the valuation of these health benefits, they could amount to as much as three to four times the cost of mitigation (Barker *et al.*, 2007).

Moderately high to high O_3 exposure imposes a loss in annual C balance of tree, with consequences for the atmospheric CO_2 balance. Tree seedlings need more light to achieve a positive C balance, and larger gaps are required. An increase in temperature is currently observed (0.5 to 0.8 °C increases, van Mantgem and Stephenson, 2007), and further increases are expected over the next century due to global warming. Leaving some pole-sized trees within large gaps will mitigate the increased temperatures associated with larger forest gaps. Moderately high to high O_3 exposure increases tree susceptibility to drought stress, with subsequent deleterious effects on forest stand susceptibility to insect and pathogen outbreaks (Grulke *et al.*, 2009). Forest management strategies to reduce individual tree level drought stress can mitigate the effects of tree susceptibility to O_3 through thinning, not just at the stand level but to ensure adequate spacing between trees. To adapt forests for the future, then, larger gaps with sparse pole-sized trees left, as well as forest patches that have been thinned will help mitigate the expected increase in drought with climate change (including the chemical environment). For aforestation efforts, drought tolerant ecotypes could be used if there are not other limiting factors (e.g., contamination of local gene pool), or more drought tolerant species appropriate to the ecological zone.

Closing gaps in knowledge

Scientific knowledge on the integrated effects of air pollutants and climate change on forests is still imperfect. To help an appropriate environmental policy-making, research and monitoring priorities are:

- At present, there are well established relationships between the exceedance of critical level/loads of pollutants and ecosystem degradation. Nevertheless, ecological interactions between critical loads and other environmental factors such as impact of increased concentrations of CO_2 and O_3, insects, pathogens, fire, drought, flooding, wind, and extreme temperatures as well as ecosystem management practices, are still poorly understood (McNulty *et al.*, submitted). There is a need to develop dynamic models for calculating critical loads, i.e. addressing changing levels of deposition and its effects, to define suitable indicators and damage thresholds, and to evaluate the combination of critical loads with other indicators of environmental stress.
- A new approach based on stomatal O_3 flux is under consideration for establishing O_3 uptake-based critical levels for the protection of vegetation (Paoletti and Manning, 2007). Such an approach should be tested on a wide range of species of conservation importance. Most observations of O_3 effects on trees have been made on northern temperate species. (Wittig *et al.*, 2009). More and longer duration open-air studies on mature trees in different forest types are critical if we are going to understand future changes to forest productivity.
- Current process models are parameterized with data taken under steady state conditions, yet environmental conditions in natural forest systems are highly dynamic. Focused research and model development incorporating stomatal responses and C balance under dynamic environmental conditions (e.g., rapid changes in light and medium term changes in humidity) will improve predictive capabilities of models.
- Assessment of the economic, human health and environmental impacts of climate change and air pollution in countries in Asia, Latin America and Africa;
- New long-term forest monitoring approaches must be developed in order to translate the atmospheric changes in climate and pollution into biological effects on forests (Fischer, 2008). Large-scale monitoring data should be available to the whole scientific community

- Extending current modelling efforts at high O_3 concentrations as expected in future scenarios. Current parameterizations have focused on forest tree responses to low to moderate O_3 concentrations.
- Researchers have provided single factor responses for modelling efforts, such that a maximum value under optimal conditions has been used for parameterization, and in a stepwise fashion, those maximum values are decreased by single factor response functions. More knowledge of synergistic interactions between limiting factors is needed for more realistic predictions of forest tree responses.

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