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Global Climate Change: Threat for the Vitality of Northern Conifers?

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Abstract

Several human activities have influenced the global climate, and the increases in atmospheric greenhouse gas concentrations as well as the rise in surface mean temperature are part of the resulting global climate change. Carbon dioxide (CO_2), methane (CH_4) and tropospheric ozone (O_3) are the most important greenhouse gases at the present time. In predicted future climate conditions, the increases in atmospheric CO_2 and tropospheric O_3 concentrations are regarded as important factors in plant responses. In spite of a number of experiments investigating the impact of changing climate on vegetation, long-term combined effects under the natural growth conditions are still poorly understood. This paper reviews the present comprehensions concerning the increases in tropospheric O_3 and atmospheric CO_2 concentrations and the rise in surface mean temperature as stress factors for the physiology of trees, focusing on the effects in most common northern conifers, Scots pine (Pinus sylvestris) and Norway spruce (Picea abies). Since the soil in northern coniferous forests is typically in shortage of available nitrogen (N) in rural areas, but exposed to N excess in most populated regions, the role of N availability as an interactive factor in plant O_3 and CO_2 responses is also discussed in this review. Additionally, most commonly used experiment facilities for evaluating the effects of air pollutants on trees are briefly introduced.

Key words: Tropospheric O_3, elevated CO_2, elevated temperature, N availability, northern conifers

Global climate change: new interest in air pollutant studies

The earth's climate has been affected by many human activities, and the increases in atmospheric greenhouse gas concentrations and mean surface temperature in the Northern Hemisphere are important part of the resulting global climate change (IPCC 2001). In addition to ongoing changes in climate conditions, low nitrogen (N) availability is typically limiting plant growth in northern coniferous forests (Helmisaari 1990, Attiwill and Adams 1993), whereas substantial areas of the most populated regions of central Europe and North America are exposed to N excess by increased anthropogenic N depositions (Fowler *et al.* 1999). Excluding some regions in southern and central Europe and wider areas in eastern Europe, those air pollutants (including sulphur dioxide (SO_2), acid rain and Suspended Particulate Matter (SPM)) under the greatest concern over ten years ago are no more regarded as a serious threat for plant health in Europe, and thus being dropped out of the main focus in European air pollutant studies (Fig. 1). Main reason for the reductions in the emissions of these air pollutants in late 1980's was tightened legislations bringing out new technical innovations and investments to the emission control. Unlike in most of the developed countries, SO_2, acid rain, SPM etc. are important air pollutants in rapidly industrializing developing countries of Asia, Africa and South America at the present time (Emberson *et al.* 2001).

During the last ten years, factors relating to global climate change have received increased attention in scientific work as well as mass media in most European countries. Increases in the concentrations of several man-made and natural greenhouse gases and their resulting effects, such as increase in mean air temperature and changes in precipitation, have been found to form a complex set of possible future climate conditions (e.g. Karlén *et al.* 1999, IPCC 2001). Within the greenhouse gases, carbon dioxide (CO_2), methane (CH_4) and tropospheric ozone (O_3) are currently regarded as the most important ones, and the increases in atmospheric CO_2 and tropospheric O_3 concentrations are found to be important in plant responses (IPCC 2001). In the terms of global climate change, nitrogen oxides (NO_x) are interest as an important group of precursors for tropospheric O_3. The increase in the concentrations of atmospheric CO_2, CH_4, and tropospheric O_3 is predicted to continue, closely relating to the increases in population and energy production as well as the rise in standard of living (For example the United States of America, having 5% of the world population, use about 25% of the total energy produced in the world) (e.g. Karlén *et al.* 1999, IPCC 2001).

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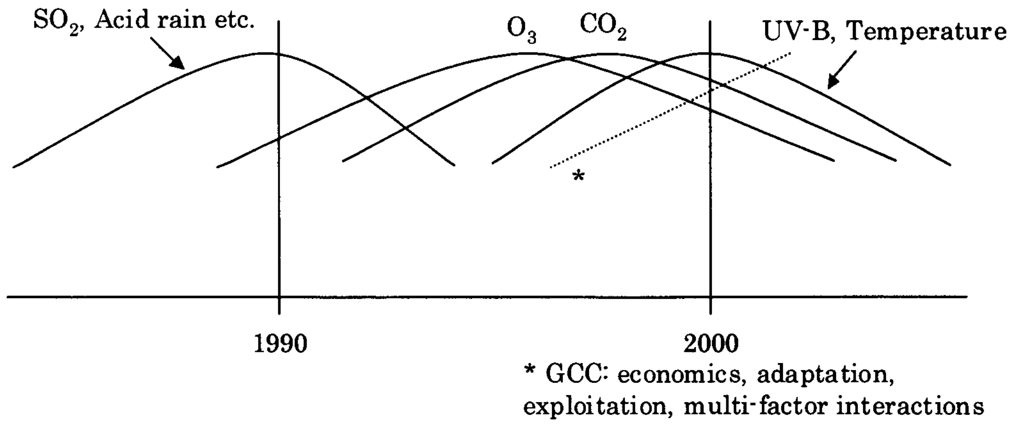


Fig. 1. Trends in air pollutant studies. Factors relating to Global Climate Change (GCC) have received increased attention (measured as governmental funding, number of ongoing projects and publications etc.) in north European air pollutant studies.

From laboratories to open-fields: advances in exposure facilities

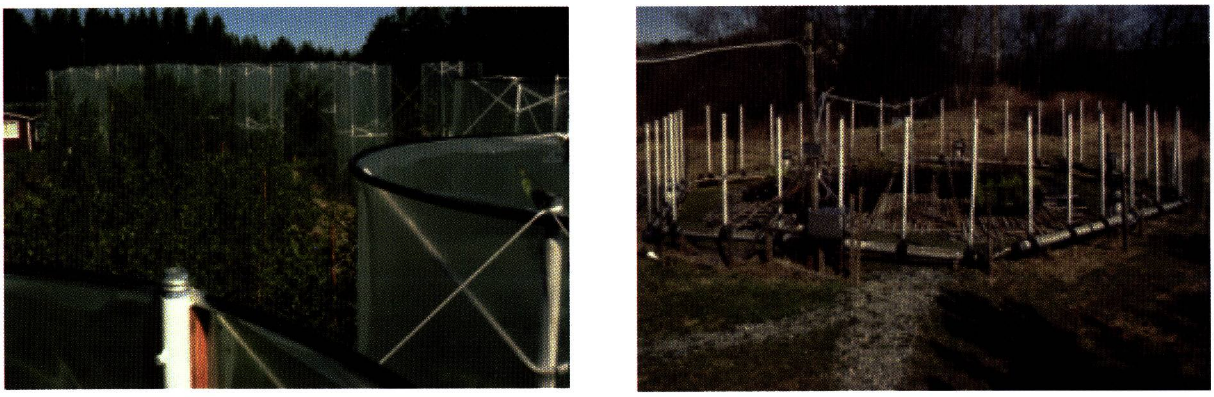
Natural plant ecosystems are typically exposed to a combination of several stress factors. Although it is well understood that the plant stress responses in controlled laboratory conditions may significantly differ from those in the field, most of the earliest experiments were conducted in glasshouses or laboratory chambers with a minimal number of stress factors in effect. However, laboratory experiments can provide useful data indicating plant processes and structures initially and most intensively affected by the studied stress factors.

Since early 1970s, open-top field chambers (OTC's, Fig. 2) offer an opportunity to study plant responses under near-ambient conditions, and long-term (several growing seasons) experiments with bigger plant species (such as trees) are also enabled (e.g. Heagle *et al.* 1973, Palomäki *et al.* 1998). A number of OTC experiments studying the effects of air pollutants on plants were conducted in Europe in 1990's, and for instance, critical O_3 levels for the vegetation in Europe have been derived on the basis of the results mainly from the OTC experiments (Fuhrer *et al.* 1997). However, experimental data from chamber-less open-field exposure facilities (Fig. 3) will be emphasized in future, since microclimate surrounding the experimental plants in OTCs is often quite artificial and a "chamber effect" caused by the differences in photon flux, temperature, humidity etc. is found in most OTC facilities (e.g. Woodward *et al.* 1991, Palomäki *et al.* 1998, Nussbaum and Fuhrer 2000). Despite more natural growth conditions and exposure patterns compared to most OTC facilities, the open-field systems have their own drawbacks also, including relative high exposure expenses and possible impact of other (non-studied) stress factors (e.g. variations in climatic conditions, insects, diseases) and effects related to the growth medium and the rooting volume in the pots (pot effect) (Arp 1991, Teskey 1995). However, most of these drawbacks can be suppressed in the field studies, for example by planting the experimental seedlings in the soil or in pots with sufficient rooting volume (e.g. 8 l for conifer seedlings) (Arp 1991, Towsend 1993).

Plant responses to elevated O_3 and CO_2 concentrations and increased temperature

Tropospheric O_3

At the present time, tropospheric O_3 is regarded as the third most important greenhouse gas after CO_2 and CH_4 (IPCC 2001). It is formed through a complex set of chemical reactions, consisting photochemical oxidation of volatile organic compounds (VOC) in the presence of NO_x (Janach 1989, Chameides and Lodge 1992). Both VOC and NO_x (nitric oxide, NO, and nitrogen dioxide, NO_2) may be of natural origin from the vegetation and soil, but most of them are a result of anthropogenic emissions from the biomass burning and combustion of fossil fuels (Fowler *et al.* 1999). In the main reaction of tropospheric O_3 production, NO_2 is photolysed by sunlight (λ<430 nm) to NO and atomic oxygen (O), which reacts with molecular oxygen (O_2) forming O_3. Part of the formed O_3 reacts with nitric oxide forming nitrogen dioxide ($NO + O_3 \rightarrow NO_2 + O_2$) and part is deposited to land surfaces. Hydrocarbons facilitate the oxidation of NO to NO_2, and build-up of O_3 is typically higher when the ratio of NO_2 to NO increases (Mustafa 1990). Although the recent data of tropospheric O_3 concentrations do not show consistent trends between the monitor sites, comparison with historical data proves a clear increase in mean surface O_3 concentration in the Northern Hemisphere (Runeckles and Krupa 1994, IPCC 2001). In plant O_3 responses, several studies have reported O_3-sensitive species among the natural vegetations as well as arable crops and trees (e.g. Runeckles and Chevone 1992, Fuhrer *et al.* 1997). Within the tree species, conifers have been shown to be more O_3 tolerant than broad-leaved trees, mainly due to lower stomatal conductance (i.e., lower intake of O_3) and the possibility of evergreens to recover during low-O_3 periods (Reich 1987, Lucas and Diggle 1997). Of the



A B

Figs. 2. A and B. Experimental facilities for the field studies in Finland.
A: Open-top chambers (OTCs) in Suonenjoki Station of the Finnish Forest Research Institute.
B: Ozone block for the O3 exposure in the open -field exposure system of the University of Kuopio.

most common conifer species in boreal coniferous zone, Scots pine (Pinus sylvestris) has been regarded as relatively susceptible and Norway spruce (Picea abies) as tolerant to O_3 (Davis and Wood 1972, Chappelka and Chevone 1992).

The main route of entry of O_3 into the plant is within the normal gas uptake via the stomata of the leaves (Polle 1998). After entering the leaf, O_3 is dissolved in apoplast and converted into reactive oxygen species (ROS), including singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), hydroxyl (OH^-) and superoxide (O_2^-) radicals (Pell and Reddy 1991, Polle 1998). Increased formation of ROS (particularly H_2O_2) in the apoplast can trigger intercellular reactions, such as hypersensitive response (HR) in an incompatible plant-pathogen interaction (Kangasjärvi *et al.* 1994, Schraudner *et al.* 1998). Whilst the HR (and further system acquired resistance, SAR) response is typical for an acute stress with high O_3 concentrations, the information about the ROS formation in chronic O_3 exposure is carried inside the cell (symplast) biochemically and by a signal transduction chain affecting cell organelles without the activation of HR response (Kangasjärvi *et al.* 1994, Sandermann *et al.* 1998, Polle and Pell 1999). Since ROS are formed also within the normal cellular metabolism under unstressed conditions, a leaf tissue is provided with a number of continuously forming and regenerating antioxidants, such as ascorbate, glutathione and polyamines, which can scavenge ROS directly or serve as substrates for several defence enzymes (Runeckles and Chevone 1992, Polle and Pell 1999). When the defence capacity of the cells is overcome, as in exposure to elevated O_3, the cell integrity can be altered and result in damage to the lipid components of membranes, reductions in amounts and activities of enzymes (par ticularly Rubisco) and disturbances in photosynthetic machinery (e.g. Runeckles and Chevone 1992, Polle 1998). Although leaf pigment and starch concentrations have reported to be affected by O_3, no clear or consistent patterns on the effects of moderately elevated O_3 concentrations on these parameters have been found in northern conifers (e.g. Robinson and Wellburne 1991, Mikkelsen *et al.* 1995, Utriainen and Holopainen 2001a, b).

Ozone-induced disturbances in the photosynthetic tissue usually result in changes in photosynthesis. In spite of a transient stimulation of photosynthesis in the newest foliage in some experiments (Wallin *et al.* 1990, Greitner *et al.* 1994, Pell *et al.* 1994), reduced rate of photosynthesis has been the most common response of trees to elevated O_3 in long-term exposures (e.g. Krupa and Manning 1988, Chappelka and Chevone 1992, Fuhrer *et al.* 1997). Ozone-induced reduction in the photosynthesis is mainly due to the direct disturbances in electron transport chain and damage to the protei n and lipid components of membranes and reductions in amounts and activities of enzymes in the photosynthetic tissues (Pell and Reddy 1991, Pell *et al.* 1997, Polle 1998). Changes in leaf photosynthesis can result in altered plant carbon allocation (Skärby *et al.* 1998, Polle *et al.* 2000). The O_3-induced changes in the carbon allocation are mainly due to the reduced rate of translocation of carbon skeletons from the leaves to the roots, reduced number of mycorrhizal root tips or accumulation of starch in foli age (Cooley and Manning 1987, Rantanen *et al.* 1994, Wellburn and Wellburn 1994). The higher retention of carbon in leaves can be due to increased carbon demand for defence or repair of damaged foliage or by disturbed phloem loading (Günthardt-Goerg *et al.* 1993, Wellburn and Wellburn 1994, Skärby *et al.* 1998). Decreased carbon allocation to the roots can be detected e.g. as a reduction in plant root to shoot ratio (Skärby *et al.* 1998, Polle *et al.* 2000, Utriainen and Holopainen 2001b).

As a result of change s in the physiological processes and carbon allocation, decreases in plant growth and biomass production are often reported under O_3-exposure (e.g. Chappelka and Chevone 1992, Fuhrer *et al.* 1997). However, the biomass production of Scots pine and Norway sp ruce seedlings has found to be affected only slightly by an open-field exposure to moderately (1.5 x ambient) elevated O_3 concentrations (Kainulainen *et al.* 2000, Utriainen and Holopainen 2000, Utriainen and Holopainen 2001a). In stem growth, the influence of O_3 on shoot length has been reported to be somewhat smaller than that on radial growth (Chappelka and Chevone 1992, Polle *et al.* 2000, Utriainen and Holopainen 2001b). In visible injury symptoms, increased leaf chlorosis and accelerated leaf senescence are found in O_3-exposed birch (Betula pendula) (Günthardt-Goerg *et al.* 1993, Pääkkönen *et al.* 1998) and beech (Fagus sylvatica) (Mikkelsen and Heide-Jørgensen 1996, Bortier *et al.* 2000), whereas the increases in yellowing and abscission of older needles are typical for O_3 exposed Scots pine (Utriainen *et al.* 2000, Utriainen and Holopainen 2000). The visible injury symptoms of O_3 in broad-leaved trees and conifers may not be directly comparable, as chronic O_3 exposure can lead to damage without visible foliar injury in stress tolerant species, and visible symptoms and needle senescence in conifers may differ from those of broad-leaved trees due to the different growth strategies and O_3 sensitivities (Pye 1988, Chappelka and Chevone 1992, Selldén and Pleijel 1995).

Elevated CO_2 and increased temperature

Carbon dioxide is currently regarded as the most important greenhouse gas. The concentration of atmospheric CO_2 is estimated to be twofold of that in the preindustrial concentrations by the end of the 21st century (IPCC 2001). Several studies have reported increased net photosynthesis and reductions in stomatal conductance and rate of dark respiration as the primary effects of elevated CO_2, resulting in increases in height growth and biomass production at a whole-plant level (e.g. Woodward *et al.* 1991, Barnes and Pfirrman 1992, Teskey 1995). There are also experiments showing down regulation of photosynthesis and reduced growth benefit (sometimes referred to as acclimation) as the CO_2 exposure is extended to more than one growing season (Woodward *et al.* 1991, Epron *et al.* 1996, Jach and Ceulemans 1999). However, the down regulation in photosynthesis is common for slow-growing evergreens, being much lower or even negligible in plant species with indeterminate growth and ability to produce new sinks for additional carbon throughout the growing season (Kaushal *et al.* 1989, Farrar and Williams 1991, Lippert *et al.* 1996). Suppressed photosynthesis is related to negative feedback on enzymes involved in sucrose synthesis and transport, direct structural changes in chloroplast membranes and decreases in leaf chlorophyll and Rubisco concentrations (Cave *et al.* 1981, Farrar and Williams 1991, Utriainen *et al.* 2000). These physiological responses are caused mainly by the accumulation of carbon in source tissue due to imbalance in source-sink relations or disturbed phloem loading or transport (Arp 1991, Farrar and Williams 1991, Woodward *et al.* 1991).

It could be hypothesised that the increase in atmospheric CO_2 concentration is able to reduce the negative impact of air pollutants on plants by decreasing stomatal conductance and providing more substrates for repairing injured tissues due to increased availability of carbohydrates (Woodward *et al.* 1991, Polle and Pell 1999). Corroborating with this hypothesis, increased defence against the O_3 stress by elevated CO_2 has been reported in plant species with a relatively high stomatal conductance (Barnes and Pfirrman 1992, Volin and Reich 1996, Turcsányi *et al.* 2000). However, most of the studies with Scots pine and Norway spruce have shown that elevated CO_2 does not provide any additional protection against O_3 damage (Pérez-Soba *et al.* 1995, Pfirrmann *et al.* 1996, Utriainen *et al.* 2000), or that elevated CO_2 may even exacerbate the negative effects of O_3 (Polle *et al.* 1993, Lippert *et al.* 1996). Different responses between the conifers and fast-growing plant species are mainly due to lower stomatal conductance and continuous pattern of shoot and root growth in evergreens, but it can also be related to the changes in root growth caused by the limited pot size (pot effect) or different nutrient regimes in the experiments (Arp 1991, Ceulemans and Mousseau 1994, Griffin *et al.* 1995) Moreover, the disadvantages relating to exposure facilities (especially lower photon fluxes inside the chambers in laboratory and OTC experiments) can easily modify plant responses to elevated CO_2 (e.g. Murray *et al.* 1996, Palomäki *et al.* 1998, Nussbaum and Fuhrer 2000).

An important consequence of the increases in greenhouse gas concentrations is the rise in global mean air temperature (often referred as greenhouse effect). Warmer weather is usually firstly mentioned in describing the global climate change, and in fact, people often use "global warming" as a synonym for "climate change" (Kempton 1997). Although there are several uncertainties in measuring and predicting the global warming, current estimations expect about 2-4 °C increase in mean surface air temperature in northern latitudes by the end of the 21st century (Krupa 1997, Karlén *et al.* 1999, IPCC 2001). Increased temperature can stimulate growth of meristems and organs accelerating plant development, but the total growth phase may be shortened resulting in fewer and smaller organs and reduced biomass accumulation (e.g. Farrar and Williams 1991, Morison and Lawlor 1999). In addition, decreased photosynthesis by the temperature elevation and acclimation to higher temperature have been reported in conifers (Wang *et al.* 1995, Wang and Kellomäki 1997, Teskey and Will 1999). However, the benefit of northern conifers from increasing temperature can be higher compared to those evergreens favouring milder temperature regions. In fact, it is reported that Scots pine and Norway spruce growing in relative cool boreal conditions can more effectively exploit the increase in temperature than the increase in atmospheric CO_2 concentration (Sallas *et al.* 2002). In addition, greater migration of plant species due to the temperature increase can be expected in northern latitudes (e.g. Roberts 1989, Huntley 1991).

Nitrogen availability modify plant O_3 and CO_2 responses

Nitrogen is the most limiting factor for plant growth in natural terrestrial ecosystems (Vitousek and Howarth 1991, Attiwill and Adams 1993). In northern conifers, current-year needle N concentrations of around 12 mg g^{-1} (Helmisaari 1990, Tikkanen and Raitio 1990) indicate N limitation, since the needle N concentrations above 15 mg g^{-1} are considered optimal for growth in most conifers (De Vries and Latour 1995). Forests in most polluted areas of North America and central Europe can be exposed to N excess due to anthropogenic N depositions up to 50-75 kg ha^{-1} yr^{-1} (Nihlgård 1985, Fowler *et al.* 1999), but the N depositions under 10 kg ha^{-1} yr^{-1} in north Europe are not yet likely to affect the N cycling in northern coniferous forests (Mälkönen *et al.* 1990).

In O_3 responses of broad-leaved tree species, increased O_3 effects by the N limitation is reported in birch (Pääkkönen and Holopainen 1995, Landolt *et al.* 1997) and hybrid poplar (Populus trichocarpa x maximowizii) (Bielenberg *et al.* 2001), but not in aspen (Populus tremuloides Michx) (Greitner *et al.* 1994, Pell *et al.* 1995, Volin and Reich 1996). Somewhat similar response pattern to that with aspen is found in conifers, as the strongest O_3-induced effects on growth or photosynthesis of Norway spruce (Lippert *et al.* 1996), Scots pine (Utriainen and Holopainen 2001b) and Loblolly pine (Pinus taeda) (Tjoelker and Luxmoore 1991) seedlings were reported in sufficient N availability. In addition, Kainulainen *et al.* (2000) found no clear interactive effects of elevated O_3 and N limitation in Scots pine and Norway spruce seedlings after two growing seasons of open-field exposure. There can be several explanations for the slight O_3 responses in N-deficient conifers, such as adaptation, increased necessity to also maintain old and injured needles under N limitation, or that the impact of elevated O_3 on growth is masked by N deficiency. However, we found clearest O_3-induced structural changes in the photosynthetic mesophyll tissue of Scots pine needles in N deficiency, indicating increasing role of N limitation in plant O_3 responses as the exposure is extended to last more than three growing seasons (Utriainen and Holopainen 2001b). Overall, our results from the open-field experiment with Scots pine seedlings indicate different strategies for low and high N conifers to cope with the O_3-induced oxidative stress; low-nutrient seedlings tend to maintain also the older needles to ensure sufficient photosynthetic production, whereas high-nutrient seedlings shed the ageing needles to allow assimilate translocation to new shoots (Utriainen and Holopainen 2001b). A similar strategy for coping with increased oxidative stress is earlier reported in birch by Matyssek *et al.* (1997).

Only slight responses to elevated CO_2 concentrations have been reported in relatively nutrient deficient Scots pine and Norway spruce seedlings (e.g. Pérez-Soba *et al.* 1995, Pfirrmann *et al.* 1996, Utriainen *et al.* 2000). This can be related to N limitation, since N-deficient plants cannot increase carbon assimilation as much as those with sufficient or optimal N regimens due to a relatively narrow range in plant tissue carbon to nitrogen ratio (e.g. Sage *et al.* 1989, Marschner 1995, Drake *et al.* 1997). Reduced N concentrations in leaves of the newest shoots by elevated CO_2 have been reported in some experiments, explained by dilution or translocation of resources to the roots to satisfy increased nutrient demand in elevated CO_2 concentration (e.g. Barnes and Pfirrman 1992; Lippert *et al.* 1996; Cotrufo *et al.* 1998). In order to optimise resource use, plants can in some extent reallocate resources from the photosynthetic processes to other processes, e.g. by liberating the excess N from photosynthetic pigments (Sage *et al.* 1989, Tissue *et al.* 1996, Utriainen *et al.* 2000). However, plant responses to elevated CO_2 concentrations are normally strongly regulated by the plant or soil N availability.

Conclusions

Atmospheric CO_2 and tropospheric O_3 are currently regarded as the most important greenhouse gases in plant responses. Additionally, increase in mean surface temperature can significantly affect plant growth especially in northern latitudes. Several open-top chamber and open-field studies have revealed that a chronic exposure to realistically elevated O_3 concentration can disturb the normal functions of relatively stress-tolerant conifers. However, O_3-induced effects on northern conifers are typically slight compared to those in broad-leaved plant species, mainly due to lower stomatal conductance of conifers and the possibility of evergreens to recover during low-O_3 periods. There is also experimental evidence that the growth-promoting effect of elevated CO_2 can be diminished in slow-growing conifers as the exposure is extended to last several growing seasons, and that elevated CO_2 cannot provide additional protection against the O_3-induced effects on most conifer species. Instead, plant N supply clearly modifies tree O_3 responses and the high and low N plants have different strategies to cope with the increased oxidative stress. Overall, experimental data from open-field studies lasting more than two growing seasons is needed to evaluate the cumulative responses of trees to the predicted impact of future climatic conditions with elevated O_3 and CO_2 concentrations and an increase in mean surface temperature.

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