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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 (CO₂), methane (CH₄) and tropospheric ozone (O₃) are the most important greenhouse gases at the present time. In predicted future climate conditions, the increases in atmospheric CO₂ and tropospheric O₃ 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 O₃ and atmospheric CO₂ 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 O₃ and CO₂ 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 O₃, elevated CO₂, 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 (Helmsaari 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 (SO₂), 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, SO₂, 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 (CO₂), methane (CH₄) and tropospheric ozone (O₃) are currently regarded as the most important ones, and the increases in atmospheric CO₂ and tropospheric O₃ concentrations are found to be important in plant responses (IPCC 2001). In the terms of global climate change, nitrogen oxides (NOₓ) are interest as an important group of precursors for tropospheric O₃. The increase in the concentrations of atmospheric CO₂, CH₄, and tropospheric O₃ 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).
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 O₃ 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 O₃ and CO₂ concentrations and increased temperature Tropospheric O₃

At the present time, tropospheric O₃ is regarded as the third most important greenhouse gas after CO₂ and CH₄ (IPCC 2001). It is formed through a complex set of chemical reactions, consisting photochemical oxidation of volatile organic compounds (VOC) in the presence of NOₓ (Janach 1989, Chameides and Lodge 1992). Both VOC and NOₓ (nitric oxide, NO, and nitrogen dioxide, NO₂) 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 O₃ production, NO₂ is photolysed by sunlight (λ<430 nm) to NO and atomic oxygen (O), which reacts with molecular oxygen (O₂) forming O₂. Part of the formed O₂ reacts with nitric oxide forming nitrogen dioxide (NO + O₂ → NO₂ + O) and part is deposited to land surfaces. Hydrocarbons facilitate the oxidation of NO to NO₂, and build-up of O₃ is typically higher when the ratio of NO₂ to NO increases (Mustafa 1990). Although the recent data of tropospheric O₃ concentrations do not show consistent trends between the monitor sites, comparison with historical data proves a clear increase in mean surface O₃ concentration in the Northern Hemisphere (Runeckles and Krupa 1994, IPCC 2001). In plant O₃ responses, several studies have reported O₃-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 O₃ tolerant than broad-leaved trees, mainly due to lower stomatal conductance (i.e., lower intake of O₃) and the possibility of evergreens to recover during low-O₃ periods (Reich 1987, Lucas and Diggie 1997). Of the...
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 \( \text{O}_3 \) (Davis and Wood 1972, Chappelka and Chevone 1992).

The main route of entry of \( \text{O}_3 \) into the plant is within the normal gas uptake via the stomata of the leaves (Polle 1998). After entering the leaf, \( \text{O}_3 \) is dissolved in apoplast and converted into reactive oxygen species (ROS), including singlet oxygen (\( \cdot \text{O}_2 \)), hydrogen peroxide (H\(_2\)O\(_2\)), hydroxyl (OH\(^-\)) and superoxide (\( \cdot \text{O}_2^-\)) radicals (Pell and Reddy 1991, Polle 1998). Increased formation of ROS (particularly H\(_2\)O\(_2\)) 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 \( \text{O}_3 \) concentrations, the information about the ROS formation in chronic \( \text{O}_3 \) 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 \( \text{O}_3 \), the cell integrity can be altered and result in damage to the lipid components of membranes, reductions in amounts and activities of enzymes (particularly 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 \( \text{O}_3 \), no clear or consistent patterns on the effects of moderately elevated \( \text{O}_3 \) 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 \( \text{O}_3 \) 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 protein 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 \( \text{O}_3 \)-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 foliage (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 changes in the physiological processes and carbon allocation, decreases in plant growth and biomass production are often reported under \( \text{O}_3 \) exposure (e.g. Chappelka and Chevone 1992, Fuhrer et al. 1997). However, the biomass production of Scots pine and Norway spruce seedlings has found to be
affected only slightly by an open-field exposure to moderately (1.5 x ambient) elevated O₃ concentrations (Kainulainen et al. 2000, Utriainen and Holopainen 2000, Utriainen and Holopainen 2001). In stem growth, the influence of O₃ 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 O₃-exposed birch (Betula pendula) ( Günhardt-Goerg et al. 1993, Pålkkönen et al. 1998) and beech (Fagus sylvatica) (Mikkelsen and Heide-Jørgensen 1996, Bortier et al. 2000), whereas the increases in yellowing and abscession of older needles are typical for O₃ exposed Scots pine (Utriainen et al. 2000, Utriainen and Holopainen 2000). The visible injury symptoms of O₃ in broad-leaved trees and conifers may not be directly comparable, as chronic O₃ 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 O₃ sensitivities (Pye 1988, Chappelka and Chevone 1992, Sellán and Pleijel 1995).

Elevated CO₂ and increased temperature
Carbon dioxide is currently regarded as the most important greenhouse gas. The concentration of atmospheric CO₂ 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 CO₂, resulting in increased in height growth and biomass production at a whole-plant level (e.g. Woodward et al. 1991, Barnes and Pfirrmann 1992, Teskey 1995). There are also experiments showing down regulation of photosynthesis and reduced growth benefit (sometimes referred to as acclimation) as the CO₂ 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 sink-source 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 CO₂ 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 O₃ stress by elevated CO₂ has been reported in plant species with a relatively high stomatal conductance (Barnes and Pfirrmann 1992, Volin and Reich 1996, Turcsányi et al. 2000). However, most of the studies with Scots pine and Norway spruce have shown that elevated CO₂ does not provide any additional protection against O₃ damage (Pérez-Soba et al. 1995, Pfirrmann et al. 1996, Utriainen et al. 2000), or that elevated CO₂ may even exacerbate the negative effects of O₃ (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 CO₂ (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 CO₂ 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 O₃ and CO₂ 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 anthropogenic N depositions up to 50-75 kg ha\(^{-1}\) yr\(^{-1}\) (Helmisaari 1990, Tikkanen and Raitio 1990) in Europe can be exposed to N excess due to 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\(^{-1}\) (Helmisaari 1990, Tikkanen and Raitio 1990), 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 (Mäkkönen et al. 1990).

In O\(_3\) responses of broad-leaved tree species, increased O\(_3\) effects by the N limitation is reported in birch (Päkkönen 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 (Lipppert 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, Kaimiläinen 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, Pfirrman 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 regimes 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 Pfirrmann 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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