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"Impacts of Air Pollution and Climate Change on Forest Ecosystems"

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Abstracts

Session I

Invited Talks

(Elena Paoletti, Chair)

IUFRO – A Vision for the future

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The International Union of Forest Research Organizations (IUFRO) was established formally in 1892, and is one of the oldest non-governmental organizations in the world. During its 116-year history, it has seen many changes, and there is no sign that these changes are abating. Today's IUFRO has two primary objectives. Firstly, it seeks to promote global cooperation in forest-related research. This has been its traditional role, and it has achieved this through meetings and the development of international protocols and agreements for forest science (the early standards for SO_2 injury to trees being a good example). IUFRO has recently become a full member of the International Council for Science (ICSU), and already the opportunities for IUFRO member organizations to develop partnerships with other disciplinary organizations is increasing. The second objective is to promote the use of science in decision-making. This occurs at all scales, but particular emphasis has been placed by IUFRO on the role of science in international policy development. As such, IUFRO is encouraging the development of science in a number of areas of concern to policy makers. These include: water resources; the livelihoods of forest-dependent peoples; research-policy connections; carbon sequestration; forest biotechnology; and endangered species and nature conservation. In each case, a Task Force is addressing the issues, provide recommendations and, if appropriate, generating a new Research Group within the IUFRO organization. Particular focus is being placed on interdisciplinary research, and IUFRO would like to see the involvement of scientists from a greater range of disciplines than hitherto. Many areas of forest research are well-developed and very significant progress has been made. For example, although many questions remain, we now know a great deal about how air pollution impacts trees, including both direct and indirect effects. IUFRO sees a need for this knowledge to be more widely disseminated – especially to those countries developing air quality problems. IUFRO scientists have an important role to play in helping achieve this aim, always considering that IUFRO represents an entirely voluntary organization.

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Air pollutants of significant importance for forest health

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Air pollutant effects on forests have all too often been focused on the effects of air pollutants on trees. However, forest health encompasses much greater complexity than trees alone, with potential for air pollutant effects on leaf surface communities, bark, ground-storey vegetation, soil chemistry, soil fungi and microbes, and soil fauna. Biological processing of deposited material, at all levels in a forest, changes the incoming (largely inorganic) pollutants into a range of different materials, which have different patterns of behaviour within the forest, and lead to changes in the effects of the forests on their surroundings, for example, downstream or downwind.

It is clear that subtle biotic interactions within a forest may have more important consequences than the direct effects of pollution – the effects on the incidence of disease or insect attack being an obvious, but poorly documented, factor. However, the ways in which the air pollution climate is changing, along with predicted broader-scale climatic changes, may have an impact on the processing of air pollutants by forests, with consequential implications for forest health.

Recent reports and models will be used to demonstrate how the threats to forest health from air pollution are changing, and to identify the research needed to address possible future issues.

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Forest health status in North America

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The forests of North America continue to provide a variety of benefits including water, recreation, wildlife habitat, timber and other forest products. However, they continue to face many biotic and abiotic stressors, including fires, native and invasive pests, fragmentation, destructive weather events, and air pollution. Forest health specialists have been monitoring the health of forests for many years. This presentation will highlight some of the most damaging forest stressors affecting North American forests in recent years and provide some projections of future risks.

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Forest health status in Europe

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Forest health status in Europe is assessed by the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). Established by the Convention on Long-range Transboundary Air Pollution (CLRTAP) under the United Nations Economic Commission for Europe (UNECE), ICP Forests has been monitoring forest condition in close cooperation with the European Commission (EC) for 20 years. On the pan-European transnational monitoring grid (16 x 16 km) several of the main species show an increase in defoliation from 1990 to 2005. This applies in particular to *Pinus pinaster* (increase from 13.2% to 18.9% mean defoliation), *Fagus sylvatica* (17.9%-22.2%), *Quercus ilex* and *Quercus rotundifolia* (13.8%-23.8%) as well as *Quercus robur* and *Quercus petraea* (21.0%-25.5%). Defoliation of *Picea abies* undulated around 23% without a clear trend. Of the main species, *Pinus sylvestris* is the only one experiencing a decrease in defoliation (24.3%-22.6%). Its recovery particularly in Poland and in parts of the Baltic States since the mid 1990s renders *Pinus sylvestris* in a slightly better condition than in 1990. Due to the severe heat and drought in summer 2003, crown condition of all main species except *Pinus sylvestris* and *Quercus ilex* and *Q. rotundifolia* deteriorated rapidly from 2003 to 2004 in southern Finland, southernmost Sweden, central and southern Germany, some parts of France and total Bulgaria. From 2004 to 2005 a recuperation was visible for *Fagus sylvatica, Picea abies,* as well as for *Quercus robur* and *Quercus petraea*. For sulphate, nitrate, ammonium, calcium, sodium and chlorine, the spatial and temporal variation of bulk and throughfall deposition was evaluated. The spatial variation was mapped for the mean deposition over the year 2001-2003. The temporal variation was calculated for the period 1998-2003. Depending on data availability, between 197 and 260 intensive monitoring plots were involved in the study. Spatial patterns of deposition can be recognized and reflect partly the regional emission situation. High sulphate deposition in coastal areas is correlated with high sodium deposition, indicating sea salt as an origin. Throughfall deposition is confirmed to be higher than bulk deposition. In the period of observation, throughfall deposition of sulphate decreased from 8.8 kg ha^{-1} a^{-1} to 5.6 kg ha^{-1} a^{-1}, while bulk deposition decreased from 6.2 kg ha^{-1} a^{-1} to 4.2 kg ha^{-1} a^{-1}. Also bulk deposition of nitrogen compounds decreased, but at a lower rate than sulphate. No clear trend is obvious in throughfall deposition of the nitrogen compounds.

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Climate change, air pollution and forest carbon sequestration**

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Atmospheric CO_2 concentrations are rising steadily over the Earth's surface and are a primary driver in global warming. Simultaneously, levels of the third most important greenhouse gas, ground-level ozone (O_3), are increasing in the troposphere in many regions around the world. While there has been a large amount of discussion about using tree plantings to sequester carbon and decrease atmospheric CO_2, little is known about the capacity of forests to sequester carbon under changing climatic conditions coupled with co-exposure to elevated levels of CO_2 and O_3. In this paper, we will present results of a nearly decade long study in northern Wisconsin that examines the impacts of elevated CO_2 and O_3, alone and in combination, on forest ecosystem productivity. For model aspen, aspen-paper birch, and aspen-sugar maple stands growing for nearly their entire life history under levels of CO_2 projected for the year 2050 and O_3 at levels now occurring over large geographic areas of forest, elevated O_3 completely offsets the gains in carbon accumulation measured under elevated CO_2 alone. We will also put this experiment in context of other global change experiments and models to predict how the carbon sequestration potential of the world's forests may change in the future.

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Session II

Invited Talks

(John Innes, Chair)

Forecasts of continental and global vegetation distribution changes related to climate change

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Dynamic General Vegetation Models (DGVM) are a relatively new concept in modeling that combines the abilities of models that simulate vegetation distribution (biogeography) with those that simulate vegetation growth and productivity (biogeochemistry) and usually also include a fire disturbance module. The MC1 model is a DGVM that combines the MAPSS biogeography model with the CENTURY biogeochemical cycling model. MC1 includes a newly built fire model that combines algorithms from several previously published models that simulate fuel loading characteristics, ground fire, canopy fire, and ecosystem effects from fire. MC1 has previously been used for assessments over the conterminous U.S. of the potential impacts of climate change. It is currently being used to produce experimental forecasts of fire risks over the conterminous U.S. for the upcoming fire season. Under the VINCERA (Vulnerability and Impacts of North American forests to Climate: Ecosystem Responses and Adaptation) project, MC1 simulated the impacts of potential climate change through the 21st century under 6 future climate scenarios. Changes in vegetation distribution, carbon balance and fire impacts will be presented from the VINCERA project. All major forested regions of North America (Boreal, Western temperate and Eastern temperate) experience the potential for increased fire, but for very different reasons and with very different carbon balance results. Fire suppression has the potential to significantly change these outcomes. A set of global scale simulations is being produced and compared with the VINCERA results. Global forests, potentially sensitive to climate change, include the Boreal, Tropical and most temperate forests, with respect to both drought and fire.

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Social issues & research needs in the urban-wildland interface

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Demographic shifts are occurring rapidly in the U.S., with movement toward urban and urban-interface areas across the country. Urban National Forests (UNFs) are those forests located within 50 miles of a population center of greater than one million people. In 1995 fourteen National Forests in eight U.S. states were identified as UNFs; since then another ten have been identified. These forests demonstrate unique management challenges and opportunities including: year-round accessibility; cultural influences, including rapidly changing demographics; emergence of new activities which often develop before management policies are established for them; and competition for open space caused by high land values, and urbanization nearby and within the forests. Other interface issues include urban social problems migrating to public lands (including crime and traffic congestion), public and employee safety issues, and the need for complex information strategies (caused by language, race/ethnicity, and class diversity). With these shifts comes an increased need for forest managers to reach out, gain the trust, and understand urban publics. To do this requires consideration of a mosaic of research topics. Recreation (the largest use of UNFs) research topics include: assess recreation needs for urban populations and examine views on natural spaces and their management; assess impacts of renovation or resource hardening at recreation sites in order to guide future management actions; monitor initial and longer-term impacts of redirection of unmanaged use; determine the supply and demand for different types of recreation activities, and the economic benefits or impacts to various stakeholders; and understand perceptions of safety on forestlands, including fire-safe practices. Other research topics include: increase understanding and use of social capital to work more collaboratively with partners and local communities; provide knowledge and tools specific to resource management related to water quality, fire, watersheds, threatened and endangered species, air quality, and human health; assess decision protocols for ecosystem services and urban infrastructure; develop tools for monitoring the impacts of outdoor recreation to develop interventions for habitat protection; and improve communication of information to the public and fire personnel before and during wildfires to reduce wildfire threats to life, property, and natural resources.

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Forty years of air pollution and its effects on southern California forests

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Since the mid-1950's native pines in the San Bernardino Mountains have shown symptoms of decline. Initial studies in 1963 confirmed that ozone was responsible for the injury symptoms observed and the decline in health of sensitive trees. The increasing number of weakened and injured trees in the Southern California Mountains resulted in extensive sanitation salvage logging between 1960 and 1980. Ambient ozone decreased significantly by the mid-1990s, resulting in decreased ozone injury and increased tree growth. Since 1990, studies by Forest Service scientists have shifted focus from ozone effects research to examining the role of wet and dry deposited acidic pollutants to ecosystems, interactions between air pollution and drought, physiological and allocation responses of air pollution affected trees, and air pollution effects on hydrological and soil processes. During this time studies found that stomatal response in air polluted forest did not follow current models, that the combination of ozone and nitrogen deposition decreased fine root biomass, altered carbohydrate partitioning within trees and changed carbon cycling within the ecosystem. During 2001-2004 a severe drought occurred in the San Bernardino Mountains that resulted in the death of about 20% of all mature trees. Mortality was most severe for pines and had the least impact on Black Oak and Incense Cedar. Mortality was highest at the highest air pollution areas, while few pines died at the lowest air pollution areas. This event has altered the focus of current studies to better understand the distribution ambient air pollution, bulk deposition and injury in southern California Mountains, and the effect that air pollution deposition has on forest composition, mortality and susceptibility to wildfire.

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Patterns of understory biodiversity in mixed coniferous forests of southern California impacted by air pollution, fire and drought

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Vegetation surveys in southern California coastal sage scrub and desert have shown that anthropogenic N deposition is related to increased abundance of exotic invasive species and decreased diversity of native species. However, a more complex pattern emerged from surveys of the diverse, herbaceous understory vegetation in mixed coniferous forest of the San Bernardino National Forest. The observed patterns result in part from interactions between the canopy trees and understory vegetation, as these vegetation layers are differentially impacted by air pollution, including both ozone and N deposition, fire, and drought. The 2002 drought and stand-replacing fires in 2003 killed many acres of trees. The result in some areas has been dense stands of invasive grasses (*Bromus tectorum* at higher elevations, *B. diandrus* at lower) that decrease the diversity of native plants. Elevated ozone has caused needle drop and deep litter layers in the western San Bernardino Mts. The extremely deep litter layer inhibits growth of most native forbs, resulting in a species-poor understory. Alternatively, understory forb richness is higher than expected in areas of intermediate N deposition. Measurements of atmospheric N in diverse understory vegetation in the San Jacinto Mts. suggest that N is being scrubbed out of the atmosphere by the trees, such that understory vegetation may have relatively little negative impact from N deposition. This suggests that the overstory is buffering the ground layer vegetation from the immediate impacts of elevated N. In N-limited soils dominated by trees there may be a lag time in response of the forbs to N deposition The resultant patterns show that air pollution gradients do not predict understory vegetation diversity as well as in less complex vegetation types, and there are interactions with fire and precipitation trends.

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Alterations of the biochemical pathways of plants by the air pollutant, ozone: which are the true gauges of injury?

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Plant strategies to survive ozone stress include exclusion or tolerance of ozone. If these processes fail, past observations of ozone injury have indicated many physiological and metabolic changes then occur; most of these changes are likely to have been initiated at the level of gene expression, suggesting signal transduction. In the last decade considerable understanding of the biochemical process within plants has been developed. Currently there are several hypotheses regarding a response of plants to ozone fumigation: [1] membrane dysfunction and alteration of purpose; [2] stress ethylene interactions; [3] impairment of photosynthesis via changes in Rubisco levels and the guard cells so that the stomata do not track correctly the environment; [4] antioxidant protection through metabolites and enzyme systems to reduce the oxidant load; and [5] general impairment or disruption of metabolic pathways.

Many believe that free radicals and other oxidative products, formed in plant leaves under ozone exposure, are responsible for much of the spread of the biochemical alterations. There are obvious chemicals which may account for the changes that are observed, such as hydrogen peroxide. Once the ozone enters the tissue, evidence suggests the first line of defense is a range of antioxidants, such as ascorbate, glutathione peroxidase, superoxide dismutase, and catalase. If overwhelmed, subsequent events occur which are highly suggestive of systemic acquired resistance. Furthermore, other defensive indicators, such as salicylic acid and jasmonic acid, tend to increase, but more slowly than ethylene, and spread their signaling effects more widely in the plant.

The primary set of metabolic reactions that ozone triggers is thought to be “wounding” responses with a secondary response of senescence. The dramatic strides in understanding the genetic make-up of plants, gene control, and signal transduction/control over the last few years will only accelerate in the future. We need now to have an understanding of those events that can be translated into more detailed schemes of how ozone alters much of the basic metabolism of plants and how plants counteract or cope with ozone. What is now known about how varied biochemicals and their pathways are changed upon ozone exposure will be discussed.

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Session III

Interactions between Air Pollution, Climate and Forest Pests

(Rainer Matyssek, Chair)

Linking increasing drought stress to Scots pine mortality and bark beetle infestations

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Temperature increase during Spring and Summer in semi-arid regions is thought to increase drought stress to trees and to favour population growth of secondary insects, such as bark beetles. However, it is almost impossible to prove such a relation at a landscape level.

In the dry Swiss Rhone Valley, Scots pines forests have experienced increasing mortality in recent years linked to increasing temperature and drought events. Although various bark beetles and other beetles are usually observed in dying trees no typical bark beetle mass infestation pattern was observed.

In our study we correlate time series of drought indices from long-term climate stations, mortality trends from a long-term observations plot and mortality probabilities modelled from tree rings with documented occurrences of insects, mostly various bark beetle species and a buprestid beetle, using forest damage reports and reports of the phytosanitary extension service.

While precipitation in the research area has little changed, increasing temperature, in particular in the last 20 years, has lead to a recent increase in drought stress indicators (precipitation minus Thornthwaite's potential evapotranspiration). At the long-term research site tree mortality over the last ten years correlated well with drought stress during the previous summer. Reconstruction of mortality probability from regional tree ring series also correlated well with drought stress indicators with an increase in both drought stress and mortality indicators since the early 1990s. Reported beetle damage to pines also increased dramatically in the 1990s. The correlation of pine beetle incidences with drought indices and growth reductions may be due to the increased susceptibility of pines, as indicated by reduced tree growth, or to increasing population of bark beetles. We tested the later in a four-year felling experiment of trees in various vitality classes. After drought years the density of colonizing beetles increased.

In summary: Increasing temperatures in the Swiss Rhone valley have most likely both weakened Scots pines and favoured bark and buprestid beetle populations leading to increased pine mortality.

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Changes in susceptibility of European beech towards *Phytophthora citricola* under the influence of elevated CO_2 and nitrogen fertilization

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Phytophthora diseases of forest trees became more serious in the last few years – e.g. *P. ramorum* causing "sudden oak death" in the US, *P. cinnamomi* infecting Eucalyptus in Australia and oaks in Southern Europe or *P. alni* on alder in Central Europe.

P. citricola, besides other *Phytophthora* species infects European beech (*Fagus sylvatica*) in all ontogenetic stages from seedlings, where it causes "damping off", up to mature trees where root and stem rot are observed. We investigated changes in the host-pathogen interaction of *P. citricola* with saplings of European beech under the influence of elevated CO_2 and/or nitrogen supply.

While elevated CO_2 increased the susceptibility and mortality of beech saplings, additional nitrogen fertilization increased resistance to some extent. Most susceptible beeches grown under elevated CO_2 and low nitrogen supply showed transiently reduced net photosynthesis rates and stomatal conductance as well as enhanced mortality within the first few weeks after inoculation. However, surviving saplings managed to tolerated a high level of *P. citricola* root infection. In consequence water use efficiency (WUE) increased during the first year of infection and was significantly higher in the second year as compared to the corresponding healthy control trees. These changes in WUE were attended by a decrease in root to shoot ratio and an increase in specific root tip densities. One of the driving factors for the enhanced susceptibility under elevated CO_2 might be changes in the species distribution of the mycorrhization.

For further investigations on the changes in susceptibility, we conducted a stable isotope labeling experiment with $^{13}CO_2$ and ^{15}N nitrogen fertilizer during the early stage of the root infection. Thus *P. citricola* infection increased the carbon allocation into leaves on the cost of roots, which in the long run could explain the decrease in root to shoot ratio. In addition, nitrogen allocation from roots to above ground biomass was reduced as well, but with different characteristics between ambient and elevated CO_2, which might be a result of the differences in susceptibility.

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Acclimation to O_3 affects host/pathogen interaction and competitiveness for nitrogen

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Interactions between pathogens and abiotic factors in plant response demand for increased awareness, as they affect competition, species composition and ecosystem functioning. The present study demonstrates such interactions in trees to be species-specific. In a two-year phytotron study, juvenile trees (3 to 6 years old) of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) were grown in mixture under ambient and twice-ambient ozone (O_3) and infested with the root pathogen *Phytophthora citricola*. We investigated the O_3 influence on the trees' susceptibility to the root pathogen and assessed, through a ^{15}N-labelling experiment, the impact of both treatments (O_3 exposure and infestation) on belowground competitiveness. The hypotheses tested were that (1) both *P. citricola* and O_3 reduce the below-ground competitiveness and (2) that susceptibility to *P. citricola* infestation is reduced through acclimation to enhanced O_3 exposure. Below-ground competitiveness was quantified via cost/benefit-relationships, i.e. the ratio of structural investment in roots relative to their uptake of ^{15}N label.

Beech had a lower biomass acquisition and captured less ^{15}N under enhanced O_3 and *P. citricola* infestation alone than spruce, whereas the latter species appeared to profit from the lower resource acquisition of beech in these treatments. Nevertheless in the combined treatment, susceptibility to *P. citricola* of spruce was increased. As beech responded negatively to ozone, these responses were not exacerbated by additional pathogen infestation. Thus in beech, acclimation to ozone may have facilitated pathogen defense. Potential trade-offs between stress defense, growth performance and associated nitrogen status are discussed for trees affected through O_3 and/or pathogen infestation. For example, in spruce, the N not used in biomass production may reflect demand and physiological costs of stress defense. With respect to growth performance, it is concluded that O_3 enhances the susceptibility to the pathogen *P. citricola* in spruce, but apparently raises the defense capacity in beech. Thus, sensitivity to O_3 appears to pre-determine the differential response to pathogen infestation under O_3 stress.

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Pre-inoculation ozone exposure predisposes oak leaves to attacks by *Diplodia corticola* and *Biscogniauxia mediterranea*

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One-year-old cork oak (*Quercus suber*) and Turkey oak (*Quercus cerris*) seedlings were exposed to ozone (110 ppb, 5 h d^{-1}, for 30 days) and were inoculated with *Diplodia corticola* and *Biscogniauxia mediterranea*, respectively, by spraying a suspension of spores on the leaves. Both fungi are endophytic and may act as weakness parasites, contributing to oak decline. Ozone exposure stimulated leaf attacks after inoculation, despite both oak species were ozone-tolerant. In fact, steady-state gas exchange, leaf waxes and wettability were not significantly affected by ozone. In *Q. cerris*, O_3 altered the structure of stomata, as observed by scanning microscopy, and reduced the leaf relative water content. No hyphal entry through stomata or growth attraction towards stomata was, however, observed. As inoculations were performed in a humid chamber, stomata were likely to be closed. When *Q. cerris* was inoculated in natural conditions, i.e. in a forest infected by *B. mediterranea*, O_3-exposed seedlings showed a higher number of *B. mediterranea* isolates than the controls, suggesting that pre-inoculation O_3 exposure predisposed *Q. cerris* leaves to attacks by *B. mediterranea* independently on stomata. In fact, the hyphae of both fungi were able to enter the leaf directly through the abaxial blade cuticle. Two ways of penetration were observed: gradual embedding into the epicuticular waxes, and production of a hollow in the cuticle at the penetration point. The main cause of the increased leaf injury in O_3-exposed seedlings appeared to be the higher germination rate of spores than in control leaves. Increased attacks after O_3 exposure may contribute to the oak declines caused by these weakness parasites in Mediterranean ecosystems.

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Session IV

State-of-Science on Concepts of Critical Loads for N, S, and Acidity and Critical Levels for Ambient Ozone

(Steve McNulty and Robert Musselman, Chairs)

The use of critical levels for determining plant response to ozone in Europe and in North America

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Critical levels to determine plant response to ozone have been used in Europe since the 1980s, utilizing the concentration-based AOT40 to relate plant response to ambient ozone exposure. More recently, there has been progress in Europe toward utilizing flux-based critical levels, because plant response is more closely related to ozone uptake than to the amount of ozone in ambient air. Flux-based critical levels are plant species specific; but data for parameterization of flux-based critical levels models is lacking for most plant species. Nevertheless, flux-based critical levels are now being used for a limited number of agricultural crops and tree species where data are available. The use of flux-based critical levels is also limited by the lack of adequate consideration and incorporation of plant internal detoxification mechanisms in flux modeling. Critical levels have not been used in North America; but recent interest in the US and Canada for using critical loads for nitrogen and sulfur has generated interest in using critical levels for ozone. A major obstacle for utilization of critical levels in North America is that ambient air quality standards for ozone in the US and Canada are concentration-based and are not specific to individual plant species. Therefore, critical levels can not be used in North American in the regulatory process for setting ambient air quality standards without legislative changes. Nevertheless, critical levels can be used to determine the impact of ozone various on plant species in different regions in North America.

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Critical levels for air pollutants to protect forest vegetation in Europe – are they still useful?

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Together with the critical load, the critical level (CLe) concept is an effects-based approach developed to assist emission control strategies in the ECE region. In this perspective, CLe is a typical example of an issue at the policy-science interface. The concept of CLe was suggested at a UN/ECE workshop held in Bad Harzburg, Germany in 1988. At that time, a critical level was defined "as the concentration of a pollutant in the atmosphere above which direct adverse effects on receptors, such as plants, ecosystems or materials, may occur according to present knowledge". This concept was further developed in a series of dedicated workshops held in Europe from 1989 to 2005. Today, the UN/ECE (2004) define the critical level as "the concentrations, cumulative exposure or cumulative stomatal flux of atmospheric pollutants above which direct adverse effects on sensitive vegetation may occur according to the present knowledge". Changes in definition were necessitated by the development of the ozone index used to characterise ozone exposure.

The CLe depends on the pollutant and on the receptor being considered and includes a variety of response parameters (e.g. growth changes, yield losses, visible injury and seed production). Today, CLe values have been set for sulphur dioxide, nitrogen oxides, ammonia and ozone in relation to different vegetation categories. When considering forest ecosystems, CLe descriptors include annual and semi-annual means (SO_2), annual and 24-hour means (NO_x, NH_3), cumulative concentration and accumulated stomatal flux over a six month period (O_3). While the benefits arising from the adoption of clean air strategies was obvious in the case of a primary air pollutants such as SO_2, O_3 poses quite different problems and represents a good paradigm of present and future challenges that are facing air pollution scientists. In this paper, current settings of CLe for forest ecosystems in Europe will be reviewed briefly. However, for the reasons mentioned above, special emphasis will be given to O_3 in order to discuss the basis for setting CLe in relation to concentration, cumulative concentration and stomatal uptake, their numerical definitions, inherent limitations, scales of application and research priorities.

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The challenge of making ozone critical levels more mechanistic

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Ozone regimes at the global scale are predicted to stay high or even increase, although scenarios may vary by region. Tropospheric O_3 is a factor of global change, with implications for the global carbon sink strength and Kyoto process. Therefore, quantitative risk assessment of carbon relations of vegetation as affected by O_3, particularly for significant components of the biosphere such as woody-plant systems, will be needed and requires increased analytical precision. Enhanced precision can only be accomplished by linking O_3 risk assessment with a reliable basis of cause-effect relationships. Given this prerequisite, the currently applied exposure-based AOTx O_3 risk assessment tool must be regarded as unsatisfactory for future assessments, because O_3 uptake rather than exposure drives plant response to O_3.

In view of the lack of a mechanistic basis for the AOTx, the O_3 flux concept has been developed to relate O_3 uptake through stomata (i.e. the physiologically relevant dose) to plant response. The flux concept represents a "phytomedical" approach, but must cope with assessment constraints such as interaction with boundary layers, non-stomatal O_3 flux and VOCs. Comparisons of the AOTx with the O_3 flux approach are limited because of the lack of data available to determine the flux-based thresholds and critical levels. Xylem sap flow measurement in tree trunks (providing whole-tree O_3 uptake) as combined with the eddy covariance approach (providing total O_3 flux into the canopy) will counteract assessment constraints by separating stomatal from non-stomatal O_3 deposition at the stand level.

However, O_3 uptake as the "physical" dose cannot be equated with the physiologically effective O_3 dose to reflect plant responsiveness per unit of O_3 flux. This ratio varies depending on defence capacity, ontogenetic and phenologic stage and plant life form, and is reflected by non-linearity in cause-effect relationships. Metabolic responsiveness to ozone is a complex process. The O_3 flux primarily acts as an inductor of defence that triggers, upon initial utilization of antioxidants present in plant tissue, self-amplification of oxidative stress ("oxidative burst"). As a result, stress signalling sets the metabolism on "alert". Thereafter, somewhat decoupled from O_3 flux itself, stress response is controlled by the plant through further oxidative self-amplification, being part of the metabolic regulation of the plant-intrinsic redox system. This chain of actions varies the plants responsiveness to O_3 so that unravelling and quantifying the involved metabolic regulation is an ultimate research aim. In summary, O_3 risk assessment must be based on both the O_3 flux (role of stomata in stress avoidance) and the effective O_3 dose (role of redox regulation in stress tolerance).

Practical application of O_3 flux-based risk assessment requires simplified estimates of the plant's defence capacity and O_3 sensitivity parallel with the O_3 flux determination, a challenge necessary before current exposure-based risk assessment can become obsolete. Conceptual models and hypotheses towards simplification will be presented, striving to unravel the common underlying principles in O_3 responsiveness across plant life forms and scenarios. Progress achieved to date using free-air O_3 release systems at actual field sites for unraveling relevant mechanisms are promising to provide scientifically credible quantifiable data on cause-effects relationships for risk assessment of forest tree and ecosystem response to O_3.

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Use of sapflow measurements to validate stomatal functions for mature beech (*Fagus sylvatica*) in view of ozone flux calculations

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It is widely recognized that the uptake of ozone through the stomata is a better measure for ozone toxicity than external concentration (Reich 1987). There are, however, still gaps in knowledge of calculation of stomatal uptake although models have been proposed (Emberson et al. 2000). With sapflow measurements it is possible to get a continuous record of transpiration even in mature trees and under undisturbed conditions. They can be used to derive canopy conductance as proposed by Granier et al. (2000) and therefore are a useful tool to validate stomatal functions.

Sap flow was measured in three beech sites in Switzerland. The derived canopy conductance was related to meteorological parameters. The time lag with the highest correlation between sap flow and meteorological parameters was dependent on sap flow velocity and on VPD deficit of the preceding days. The median value was 30 minutes. After having determined the optimal time lag, nonlinear regression was used to estimate stomatal functions for VPD, temperature, light and soil water potential. The results show significant deviations from the currently used flux model for beech which has implications for ozone flux calculations.

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Redefining critical load limits in United States ecosystems to include multiple environmental stresses: implications and solutions

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The federal agencies of the United States (US) are currently developing guidelines for critical nitrogen load limits for US forest ecosystems. These guidelines will be used to develop regulations designed to maintain pollutant inputs below the level shown to damage specified ecosystems. By traditional definition, an ecosystem is considered to be at risk when nitrogen loads exceed a critical level. The excess over the critical load is termed the accidence, and a larger exeedence is often considered to pose a greater risk of damage to an ecosystem. This definition of critical loads applies to acute or chronic individual stress impacts, but does not work well when an ecosystem is subjected to multiple environmental stresses. For example, the southeastern US mountains of western North Carolina received some of the highest rates of nitrogen deposition in the eastern US, but these nitrogen deposition levels are still considered to be below the critical load rate. The area experienced a moderate three year drought from 1999-2002. In 2001, white pine and spruce trees began to die in large numbers in the area. The initial evidence confirmed that the affected trees were killed by the southern pine beetle (SPB). This insect species is not normally successful at colonizing these tree species because heavy oleoresin production exudes the boring beetles from impacted trees. Subsequent investigations revealed that the relative ratio of above ground to below ground biomass was high compared to ratios of same species from lower nitrogen deposition areas. I believe that elevated nitrogen deposition reduced the root biomass, reduced the tree water uptake potential, reduced oleoresin production, and caused the trees to become more to susceptible to insect colonization during the drought period. If multiple stress (i.e., drought, and insects) impacts are included, then the forests in this area were in exeedence of their critical nitrogen threshold. Recent advances in ecosystem modeling of multiple stress impacts on forest ecosystems allow for more complex analysis of multiple stress scenarios. This paper explores how multiple environmental stress impacts can be assessed using computer models to determine variable critical load limits. The implications for improved forest management and pollutant regulation will also be presented.

The USDA Forest Inventory and Analysis Program and the concept of critical loads and levels: opportunities and challenges

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Abstract: At the present time the concept of critical loads and levels is becoming widely applied internationally, with the European International Co-operative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) program and recent work in Canada as prime examples. As a management guideline this concept, which in essence is no more that an a guideline as how much input of atmospheric pollution an ecosystem can sustain before adverse changes will result, is compelling. As many countries around the world move to apply this concept to forest ecosystem management the United States is hesitating even though it has a nationwide network for high quality data for deposition (National Atmospheric Deposition Network) and forest health. In this paper we provide background on the data collected by the USDA Forest Inventory and Analysis program as compared to that of ICP Forests and discuss implementing the critical loads and levels concept within USDA Forest Service, the primary management agency of forest and wilderness areas within the United States.

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Session V

Diagnosis, Monitoring and Evaluation

(Marco Ferretti and Algirdas Augustaitis, Chairs)

Overview of Lithuanian Studies:

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Step I of Lithuanian studies: trend in ambient ozone and an attempt to detect its effect on biota in forest ecosystem.

Step II of Lithuanian studies: trends in main transboundary pollutants, meteorological conditions and Scots pine defoliation: long Term study of key factors of changes in defoliation.

Step III of Lithuanian studies: does the surface ozone affect the radial increment of Scots pine (*Pinus sylvestris* L.) on territories under regional pollution load?

See Poster section for full abstracts

Ozone deposition on forests in southern Europe: risk assessment revisited

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The assessment of potential damage of ozone on vegetation requires different approaches in different climatic and environmental conditions. In Southern Europe, high ozone concentrations are frequent during summer months due to intense sunlight leading to strong photochemical activity. An ozone risk assessment approach, based on ozone concentration records, developed in Northern Europe, is in use over the whole continent. Since ozone uptake by leaves occurs through the stomata, risk assessment should be based on ozone fluxes instead of concentrations. In the particular case of a Southern European forest ecosystem, concentration-based approaches lead to important errors since concentrations are generally high in sunny conditions, corresponding to drought periods, causing stomatal closure and hence lower ozone fluxes.

Measurements of ozone fluxes and concentrations over forests (Holm Oak, Maritime Pine) in Southern Europe are presented and differences between flux-based and concentration-based ozone risk assessment approaches are critically investigated, in an attempt to improve regulatory policies.

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Ozone exposure, growth and condition of selected forests in Italy

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Ozone exposure in terms of AOT40 was estimated for 21-26 forest monitoring sites in Italy over the period 2000-2004. Diameter at breast height (DBH) was measured on all trees at the same sites in the years 1996, 1999 and 2004 and basal area increment (BAI) was calculated for all the dominant trees at each site. Crown transparency (a proxy for defoliation) was assessed for 30 trees selected among the dominant ones at each plot.

Results shows that – on average - AOT40 varies between 19 and 53 ppm h, thus largely exceeding the UN/ECE critical level (CLe_c) set to protect sensitive species under sensitive condition in Europe. With few exceptions, mean annual 2000-2004 BAI was lower than 1997-1999. Crown transparency revealed limited temporal variation.

Available site, meteorological, soil and foliar chemistry, deposition and ozone data were used according to different multivariate regression techniques to identify possible determinants of tree condition. The paper will summarize the main results obtained.

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Biomonitoring the exposition of forests to climate change and nitrogen deposition by plant phenology and mosses

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Forests are integrated into fluxes of energy and matter. In some forest ecosystems the according flux rates become critical. The presentation deals with the air temperature and the nitrogen deposition the forests in Germany are exposed to.

Mosses can be used to monitor the bioaccumulation of metals and mosses. Since 1990, the UNECE ` Heavy Metals in Mosses Surveys` provide exposure data on the accumulation of several metals in naturally growing mosses throughout Europe. Up to now, pilot studies on nitrogen accumulation were conducted in Scandinavia, in Lower Saxony and North Rhine-Westfalia (Germany) and in the Euroregion Neisse, which is part of Germany, Poland and the Czech Republic. In the latter three studies, the spatial structure of the nitrogen accumulation was analyzed by geostatistics. The interrelationships between nitrogen deposition and some site-specific and regional ecological characteristics were proved by CART and CHAID. These methods and the results corroborate that the nitrogen bioaccumulation in Germany varies at the regional scale and is rather high compared to other regions in Europe.

The rise of the air temperature is assured to be part of the global climatic change, but there is still a lack of knowledge about its spatial structure and effects at the regional scale. Thus, in the second part the presentation tackles the correlation of air temperature with the phenology of selected plants in Germany to provide a spatial valid data base for regional climate change models. To this end, data on air temperature and plant phenology, gathered from measurement sites without congruent coverage, were correlated after performing geostatistical analysis and estimation. In addition, geostatistics are used to analyze and cartographically depict the spatial structure of the phenology of plants in spring and in summer.

The statistical analyses reveal a significant relationship between the rising air temperature and the earlier beginning of phenological phases like blooming or fruit maturation. E.g., from 1991 to 1999 spring time, as indicated by plant phenology, has begun up to 15 days earlier than from 1961 to 1990. Together with the rise of the air temperature this may induce critical stress on forest ecosystems.

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The morphological sensitivity of Norway spruce and Scots pine saplings to different ozone concentrations

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The study examined ozone effects on morphological parameters of 4-year old potted Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) saplings. June 1 through June 28, 2005 the saplings were placed in 4 walk-in closed chambers of controlled environment (40 m^3 each) and exposed to ozone concentrations of 0 $\mu g/m^3$, 80 $\mu g/m^3$, 160 $\mu g/m^3$, and 240 $\mu g/m^3$ for 7 h day^{-1}, 5 days $week^{-1}$. The height of the apical shoots and the visually evaluated parameters of the foliage condition were monitored every week. After exposure half of the seedlings were destroyed and the biomass of different fractions was determined. Half of the saplings were left in the open field conditions until the spring 2006 and then the morphological parameters were assessed again. The extent of the visually estimated symptoms during fumigation tended to increase with increasing ozone concentrations, and more of the injuries were found on the Scots pine. However, the foliage of those Norway spruce saplings which were fumigated and left in the open field for the winter, in spring tended to show more of the necrosis and discoloration comparing to the Scots pine. During ozone fumigation there was no effect on the shoots length of Scots pine, but the shoots of Norway spruce in all the treatments were suppressed. The treatment by 240 $\mu g/m^3$ concentration significantly decreased the total shoot length and the biomass of the first year and older needles for both species. Besides, this concentration had a significantly negative effect on the biomass of shoots, roots and stems of Scots pine saplings. In spring 2006 the defoliation of those Norway spruce saplings that were treated by 160 and 240 $\mu g/m^3$ concentrations was statistically higher and the needles retention was statistically lower comparing to the controlled ones. Some saplings in the 240 $\mu g/m^3$ treatment even had 5-10% of dieback. The needles retention of the Scots pine was statistically lower in all the treatments.

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Meta-analysis of the responses of plant communities to the disturbance caused by point polluters

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We used meta-analysis of published data to study sources of variation in the responses of plant communities to environmental pollution. The meta-analysis combines the results of 51 field studies conducted around 50 point polluters (published between 1953 and 2005) reporting effects of pollution on richness and diversity of vascular plants. We considered the following explanatory variables: type, size and geographical position of the polluter, longevity of the impact, and richness of the original plant community. Along with responses of the entire plant communities, we separately analysed responses of woody plants (trees, shrubs), dwarf shrubs, herbs and grasses. Although pollution impact on species richness and diversity was in general negative, the effect size depended on the type of polluter, its geographical position and plant life form (ecological group). The non-ferrous smelters emitting heavy metals and aluminium factories emitting fluorine caused stronger detrimental effect compared to other sources of pollution (e.g. power plants, chemical plants). The effect size negatively correlated with the latitude at which the polluter was located: negative effects of pollution on species richness were stronger in a warmer climate, especially for woody plants and grasses. In particular, at high latitudes (over 60°) adverse effects on diversity of woody plants were not observed, and effects on richness of grasses were even positive. This finding contradicts the widespread opinion on high fragility of northern ecosystems. Regression analysis with the stepwise selection of variables ended with the model where species richness in an unpolluted (control) site explained the largest part of variation, whereas effects of climate (mean summer and winter temperatures, precipitation) did not contribute to this variation. This result suggests that species-rich plant communities experience stronger disturbance under pollution impact than species-poor communities, the conclusion contributing to long-lasting discussion on the relationships between diversity and stability.

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Session VI

Mechanisms of Action and Indicator Development

(Madeleine Günthardt-Goerg, Christian Andersen and Jesada Luangjame, Chairs)

Changes in essential oil composition in the needles of Scots pine (*Pinus sylvestris* L.) growing in the areas affected by industrial pollution

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Climatic and anthropogenic factors, such as air pollution lead to biochemical responses in a tree. Pollens and seeds of the pine are dispersed by wind that is why the role the essential oils in the needles cannot be related to the attraction of insects and other animals and might be quite unambiguously connected with the protection against pathogenic bacteria and fungi also parasites.

Changes in the amounts of secondary metabolites may be early indicators of invisible injuries. The aim of our study was to evaluate percentage composition of the essential oils for the needles of Scots pine (*Pinus sylvestris* L.) growing in the impact zones of the main factories in Lithuania – a nitrogen fertilizer factory (NFF), a cement factory (CF), an oil refinery (OR). Forests on arenosols (near NFF), luvisols (near OR), histosols (near CF) were examined. Selection of sites was based on availability of the stands and prevailing wind direction from each pollution source. Totally 14 pine stands were examined along transects from the factories. Current-year and one-year-old needles of 8 pines in each site were sampled in July, 2005. Volatile components of the needles were extracted and analyzed by GC and GC/MS. The percentage composition of the essential oils was calculated.

Over 70 components of the essential oils were identified in the needles. The needles from the selected sites differed significantly in the amounts of Bornyl acetate, β-Selinene, δ-Cadinene, Spathulenol, epi-α-Muurolol + α-Muurolol, Manoyl oxide. For the indication of the effect of the pollution current-year needles were more informative than one-year-old ones. In the sites closest to the factories statistically significant changes in percentage concentrations of monoterpens, oxiterpens, sesquiterpens, oxysesquiterpens were documented. Amounts of these metabolites correlated significantly ($p<0.05$) with the distance of the pine stands from the factories. Determined changes in the proportion of components of the essential oils in the needles of the trees affected by the industrial emissions may play role modifying susceptibility of the pine stands to the biotic factors.

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Parameterisation of the stomatal component of the DO_3SE model for Mediterranean forest trees

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Ozone effects on vegetation are more closely related to the ozone dose absorbed through the stomata than to ozone exposure in the atmosphere. Therefore the Convention of Long-Range Transboundary Air Pollution (CLRTAP) of the United Nations Economic Commission for Europe (UNECE) is moving from a concentration-based critical level towards a flux-based approach for the establishment of ozone critical levels to evaluate the risk of negative impacts on vegetation across Europe. A stomatal flux-based critical level has been recently adopted for agricultural crops. However, further information is needed before developing flux-based critical levels for forest trees and semi-natural vegetation. In particular, for Mediterranean forest trees, many uncertainties still remain for modelling the stomatal behaviour depending on environmental and phenological changes.

In this study, data collected from the literature together with previous studies performed with *Pinus halepensis* seedlings growing under experimental conditions and *Quercus ilex* adult trees growing in the field were used to re- parameterise the stomatal conductance model incorporated within the EMEP DO_3SE deposition module for Mediterranean evergreen trees. Modifications of g_{max}, f_{min}, and new f_{VPD}, f_{temp} and f_{phen} functions were developed according to either *Q. ilex* data or all data available from different evergreen species. Possible approximations to an f_{SWP} function are discussed as well. The performance of the new re-parameterised model was tested using two new data sets of stomatal conductance values measured on two populations of *Quercus ilex* adult trees growing in two locations in Spain differing in elevation and climatic conditions. Diurnal courses of stomatal conductance were followed from sunrise to sunset under ambient conditions using an open photosynthesis monitoring system (Li-Cor 6400). Measurements were performed seasonally covering the phenological changes occurred along the year. The performance of the stomatal conductance model considering either a species specific re-parameterisation or a generic "model" parameterisation for Mediterranean evergreen was tested. Moreover, the feasibility of using a "model" tree parameterisation for calculating ozone fluxes and risk assessment of ozone to Mediterranean evergreen vegetation is discussed along with the identification of those factors most important in calculating ozone flux absorbed through the stomata.

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Quantifying short term O_3 exposure effects on the level of nighttime transpiration

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A novel gas exchange system that concurrently supplies known O_3 concentrations, and measures H_2O, O_3, and CO_2 flux ("HOC" system) to leaves was used to assess short term O_3 exposure effects on the level of nighttime transpiration. Two experiments were conducted. In the first, we tested the effect of short term acute O_3 exposure on nighttime transpiration in California black oak (deciduous, *Quercus kellogii*) and blue oak (evergreen, *Quercus douglasii*) exposed previously to either charcoal-filtered air, or chronically elevated O_3 for 8 h per day (70 ppb) in open-top chambers. Both chronic (70 ppb daily for 1 and 2 months, respectively) and acute (~180 ppb, 1 h) effects were tested for simple additive or synergistic effects. In the second experiment, we tested for the effect of a range of short term O_3 exposures, to determine whether there was an inciting O_3 concentration above which significant nighttime transpiration was induced ("threshold" effect), and how long significant nighttime transpiration persisted ("memory" effect). A range in O_3 concentrations from 0 to 180 ppb for 1 h was used to elicit responses. In both the first and second experiments, individual leaves were exposed to either O_3-free air (using a commercially available gas exchange system), or elevated O_3 concentrations (using the HOC system) for one hour. During the night after the daytime exposure, stomatal conductance was measured on both the unexposed and exposed leaves. In order to test for "memory" effects, stomatal conductance was measured again the second and fourth nights with no further daytime O_3 exposure.

In California black oak, nighttime transpiration was elevated after chronic, moderate O_3 exposure (1.8 fold increase over background). A one hour acute O_3 exposure yielded no significant effects on nighttime transpiration. In blue oak, chronic O_3 exposure significantly increased nighttime transpiration (2 fold increase over control leaves). Acute, short term O_3 exposure had an even greater effect on nighttime transpiration (3 fold increase over control leaves). Chronic O_3 exposure may elevate antioxidant concentrations, permitting some protection against short term, acute O_3 exposure, because there were no synergistic effects of acute O_3 exposure in plants previously exposed to chronic treatments in either oak species. Both species had a "threshold" O_3 concentration of a one hour exposure to 150 ppb. One hour O_3 exposures greater than 150 ppb increased nighttime transpiration linearly. Different O_3 metrics will be used to present threshold responses, including O_3 exposure (dose, O_3 concentration x time), calculated O_3 uptake (O_3 concentration x gs x constant to convert diffusivity of water to O_3), and measured O_3 uptake (using the HOC system). When elevated nighttime transpiration was elicited, the response lasted for two nights after exposure.

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Gravitational infusion of ethylenediurea (EDU) into trunks protected adult ash trees from foliar ozone injury and highlighted the mechanisms of protection

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Much has been written about the effects of ozone on growth of forest trees, but conclusive proof that ambient levels of ozone affect growth of forest trees remains elusive. The methodologies used included reductionist chambers or semi-reductionist open-top chambers, and seedling or sapling trees, which precludes extrapolation of results to adult trees in real world conditions. Ethylenediurea (N-[2-(2-oxo-1-imidazolidinyl)ethyl]-N'-phenylurea), abbreviated as EDU, used as a foliar spray or soil/potting medium drench, is systemic and persistent in plants, and has been widely used to prevent foliar ozone injury and determine ozone effects on growth and yield of many herbaceous plants and some woody plants. Several investigators have used stem injections of EDU with tree seedlings to demonstrate EDU uptake and protection against ozone injury, with varying degrees of success. Interest in gravitational methods of introducing chemicals into mature trees was renewed in the 1990s when widespread outbreaks of the insect *Cameraria ohridella* occurred in horse chestnut trees in Europe. Systemic insecticides were gravitationally infused into infested trees and insect management was successful. Like pressure or low-pressure injections, gravitational infusion requires making an entry hole in a tree trunk and provision of a reservoir of the chemical that is taken up by transpiration of the tree.

Adult ash trees (*Fraxinus excelsior* L.), known to be sensitive or insensitive to ozone, determined by presence or absence of foliar symptoms in previous years, were treated with EDU at 450 ppm by gravitational trunk infusion on six occasions at 21-day intervals in summer 2005 at Turin, Italy. Our aim was to determine if sensitive trees could be protected from foliar ozone injury and which were the possible mechanisms of protection. At the end of the season, foliar ozone injury on EDU-treated trees was not complete, but was greatly and significantly reduced when compared to results from trees infused with water. Significant symptom reduction occurred at any crown level in the treated trees suggesting that EDU protected whole crowns. The amount of EDU needed to provide protection is assumed to be in the range 13-26 mg m^{-2} leaf. Protection mechanisms and possible side effects of EDU were investigated by measuring gas exchange, water relations and some biochemical parameters. Analysis of these data is still in progress.

The advantages provided by this approach are that it is inexpensive and simple, artificial chamber conditions are avoided, and both young and adult trees can be treated. The disadvantages are that gravitational stem infusion is time-consuming (1 to 7 days until uptake stopped), and numerous stem wounds advise against long-term applications. Our results indicate that further work on EDU effects and application techniques are warranted to develop a better method for using EDU in quantitative assessment of tree responses to O_3. Soil applications may be easier and as effective, without wounding trees.

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The effects of tandem summer ozone and winter thaw treatments on biomass and carbohydrate partitioning xylem cavitation and dieback in yellow birch saplings

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Potted saplings of yellow birch were exposed during the growing season to various concentrations of ozone using open topped chambers for two days per week. Between fumigations the chambers were removed to minimize chamber effects. After hardening for winter, these same plants were exposed to simulated winter thaws of different durations. This was done to determine the effect of the two stressors and their combined effects on growth, photosynthesis, leaf retention, xylem cavitation, embolism recovery as well as biomass and carbohydrate partitioning between leaf age classes stems and roots. Significant effects of ozone treatments concentrations were found on relative growth rates of stems and roots as well as root to shoot biomass ratios. A significant linear reduction in net photosynthesis with accumulated ozone exposure (ppmh) in both preformed leaves and neoformed leaves. Leaf retention was also inversely related to ozone exposure. Sugar partitioning was also significantly affected by ozone exposure and there was a significant ozone / winter thaw duration interaction on root carbohydrates. Effects of thaw duration on cavitation and xylem embolism and root damage will be discussed in relation to the potential for ozone induced predisposition of yellow birch to winter injury caused by lack of winter xylem embolism recovery.

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Ozone or drought symptoms? Diagnosis of stress factors in field samples of beech collected during the dry and hot 2003 summer

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During the hot and dry summer of 2003, forests in central Europe were exposed to elevated levels of drought and ozone stress. As one consequence (among others) of drought, stomata on leaf lower side are expected to close leading to a reduction in ozone uptake. This raises both methodological and scientific questions: 1) how can we distinguish between the effects of drought and ozone induced stress under field conditions? 2) how do both stress factors interact? In this study, we assessed beech trees growing within seven Swiss long-term forest ecosystem research plots (LWF/ICP-Forests Level II plots). Visible symptoms were analyzed in leaves taken from light exposed branches which were sampled from randomly selected trees per plot. They were validated using microscopical analyses and changes in the leaf content of condensed tannins and pigments were measured with spectrophotometric techniques. All data were analyzed with statistical methods from numerical ecology. During the 2003 vegetation season, the temperature increased by 1.7 degrees, precipitation was reduced by 44 % and the ozone dose was 1.5 times higher (based on meteorological mean values from 1998 to 2004). Drought stress was indicated by severe leaf curling and defoliation, both of which increased towards the shoot basis. Ozone stress was shown by bronzing and interveinal dark brown stippling especially in leaves at a lower shoot position. Microscopically, stress and defense reactions were especially increased in the better light-exposed tissues in the case of visible ozone symptoms, and in tissues along the water pathway in leaves showing drought stress. With increasing symptom intensity, the content of photosynthetic pigment in the leaf was reduced and that of condensed tannins increased. Chlorophyll loss more prominently contributed to changes in leaf color but in a less specific way than the condensed tannins. In conclusion, the effects of drought versus ozone stress could be qualitatively and quantitatively distinguished using cross-analyses of results from different analytical approaches.

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Response to ozone uptake in forest trees: scaling from cell to stand level at Kranzberg Forest.

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As in medicine, the risk of anthropogenically enhanced tropospheric ozone concentrations for vegetation can only be estimated by calculating "effective doses". The effective dose for ozone depends on the plants ozone exposure and stomatal uptake as well as its sensitivity. Ozone sensitivity relies on the antioxidative defense capacity and the physiological reactions induced by exceeding ozone molecules or follow-up products.

Results of the free-air ozone fumigation experiment at Kranzberg Forest show that the responses of adult trees of *Fagus sylvatica* and *Picea abies* to doubled external ozone concentrations are highly variable. After seven years under survey, significant ozone effects are mainly found on cell and leaf level but less on whole-tree and stand level. Furthermore, effects vary between measuring dates during the vegetation periods and between years. Nevertheless, some examples can be shown for consistent reactions across tree-internal levels.

The dry summer of the year 2003 stressed the important role of stomatal regulation for the ozone response of beech and spruce. The relationship of soil water content and stomatal conductance found at Kranzberg Forest can improve modelling of ozone uptake for the two species. Modelling of ozone sensitivity is much more difficult due to the high variability of defensive compounds and ozone induced physiological reactions. Consequences for the "effective dose"-concept are discussed.

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Session VII

Atmospheric Deposition, Soils and Nutrient Cycles

(Dale Johnson, Chair)

The Fernow Watershed Acidification Study: results from the first 15 years

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To assess the long-term effects of acidic deposition, results from a 15-year, whole-watershed fertilization (NH_4SO_4) experiment are used to examine the consequences of accelerated acidification on a deciduous forest ecosystem in central Appalachia. Changes in the chemistry of soil solution and stream water are consistent with conceptual models of ecosystem acidification. However, temporal changes in soil chemistry are uncertain due to a small sample size and high spatial variability. From limited soil data collected pre-treatment, a trend during the first 5 years of the experiment of declining exchangeable concentrations of Ca^{++} and Mg^{++} in surface soils while acidity increased. A rapid change in surface soil chemistry may be supported by temporal changes in soil solution chemistry. Within the first 3-4 years the concentrations of Ca^{++}, Mg^{++}, and acidity increased in solutions collected beneath the A and B horizons. In the next 3-4 years, the levels of Ca^{++} & Mg^{++} in these solutions declined while those in water leaching from the C horizon increased. In the last 7 years, levels of Ca^{++} and Mg^{++} in water leaching from the C horizon decreased. Since fertilization began, baseflow pH in stream water has declined from 6 to 5.5, and the concentrations of NO_3^-, SO_4^{--}, Ca^{++}, and Mg^{++} increased. In recent years, the concentration of NO_3^-, Ca^{++}, and Mg^{++} in stream water appears to have leveled off, and may be declining. Long-term monitoring and tree ring analyses suggest that fertilization initially increased forest growth but that growth is no longer stimulated and may be declining for several important tree species including red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and yellow poplar (*Liriodendron tulipifera)*. If acidification due to atmospheric deposition mimics these results, significant changes in forest structure and function could occur.

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Nitrogen status of forest soils in Finland: does nitrogen deposition pose a threat to forest ecosystems?

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The dramatic reductions in sulphur emissions achieved during the past 15 years have, to some extent, alleviated concern about the acidification of forest soils. However, forest ecosystems in many parts of Europe are still exposed to considerable loads of acidifying deposition in the form of nitrogenous compounds (e.g. NOx and NH_3). Forest soils in central and northern Fennoscandia are relatively deficient in nitrogen in an available form (i.e. NH_4^+ and NO_3^-), and the low nitrogen availability is considered to be the main growth-limiting factor in coniferous stands especially. However, it is possible that a continuous input of nitrogen into nitrogen-deficient forest ecosystems will, at some point in time, reach the so-called nitrogen saturation point. In this study, the effects of a continuous load of nitrogen deposition on the C/N ratio of the humus layer and the NH_4 and NO_3 concentrations in percolation water in 7 Scots pine and 6 Norway spruce stands in different parts of Finland were investigated. Annual nitrogen deposition in bulk deposition and stand throughfall, and annual mean ammonium and nitrate concentrations in percolation water (5, 20 and 40 cm depth), were monitored during the period 1996-2003. The C/N ratio was also determined on organic layer samples taken in 1996, 1999 and 2003 on the same plots.

Annual nitrogen deposition during the period 1996-2003 was about 3 – 4 kg/ha in southern and 1 – 2 kg/ha in northern Finland. During the period the mean C/N ratio of the organic layer in the pine plots was 42 and in the spruce plots 36. No appreciable changes occurred in the C/N ratio during the period 1996-2003 on any of the plots. The ammonium concentrations in percolation water remained below 0.2 mg/l, and the nitrate concentrations below 0.05 mg/l, throughout the period. The continuing relatively high C/N ratio in the organic layer indicates that there is no immediate danger of the nitrogen saturation level (i.e. C/N ratio of below 25) being reached in these sites in the immediate future.

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Modeling of nitrogen dynamics in an Alpine forest ecosystem on calcareous soils: A scenario-based risk assessment under changing environmental conditions

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The general objective of the research project was to evaluate the likely behavior of an Alpine forest ecosystem on calcareous soils under changing environmental conditions considering climate and atmospheric N deposition. The study site in the Tyrolean limestone Alps (Austria) is an intensively monitored research site with time-series data of key elements of the N cycle as well as detailed on-site climate data. Tree species composition consists mainly of Norway spruce (*Picea abies* [L.] Karst.) with some admixed beeches (*Fagus sylvatica* L.). The risk assessment was modelled on the time period 2000 to 2050 and the scenarios were: (i) current climate and current N-deposition (18 kg N ha^{-1} a^{-1}), (ii) warmer climate (+2.5 °C mean annual temperature) and N-deposition reduced by 50 %, (iii) warmer climate and doubled N-deposition and (iv) warmer climate and N-deposition as actual. We were particularly interested in possible effects on N-leaching, gaseous emissions of N_2O and in the response of forest productivity and potential species composition under the above circumstances.

Key element of the research approach was the combined application of various ecosystem simulation models to analyze system behavior. The models used were PnET-DNDC (short-term N cycling), BROOK90/HYDRUS (water balance) and PICUS v1.3 (forest productivity, species composition). With the NBM (N balance model) approach a consolidation of the three models was performed and the findings were evaluated with TRACE (mid- to long-term N cycling) and ANP (Analytic Network Process).

It became obvious, that a temperature increase and higher nitrogen input affect parts of the ecosystem and the following are examples:

- A temperature increase leads to a significant increase of the mineralization and nitrification rates. N deposition affects these processes to a minor degree.
- The nitrate leaching is elevated under the current N deposition and especially under doubled N depositions.
- The nitrate produced by microbial processes is extremely exposed to leaching whenever a rise in temperature occurs.
- The N_2O emission rates from the soil are elevated especially when the temperature increases, but also, to a lesser degree, under elevated N inputs.
- A temperature increase effects that the competitiveness of Norway spruce is diminished compared to beech and fir.

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Air pollution and watershed research in the central Sierra Nevada of California: nitrogen and ozone

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Maintaining healthy forests is the major objective for the Forest Service scientists and managers (U.S. Department of Agriculture). Air pollution, specifically ozone and nitrogen (N), may severely affect the health of forest ecosystems in the western United States. Thus the monitoring of air pollution concentration and deposition levels, as well as studies focused on understanding effects mechanisms, are essential for evaluation of risks associated with their presence. Such information is essential for development of proper management strategies for maintaining clean air, clean water and healthy ecosystems on land managed by the Forest Service. We will report on the past three years of research in the central Sierra Nevada of California, a semi-arid forest at elevations of 1,000 to 2,700 m. Information on ozone and nitrogenous air pollutants is obtained from a network of 18 passive samplers and three continuous ozone samplers. We will relate the atmospheric nitrogen concentration and dry deposition values to nitrogen concentrations in streams, shallow soil water, and precipitation within the associated Kings River Experimental Watershed. It also contains an intensive site that is part of the new Forest Service's effort to calculate critical loads to forest ecosystems. The passive sampler design allows for extensive spatial measurements while the watershed experiment provides intensive spatial data for analysis of ecosystem processes.

In the semi-arid forests of the Sierra Nevada, a large portion of N is deposited as ammonia or nitric acid in the dry summer season. These pollutants are generated by mobile sources (trains, automobiles and trucks) and agricultural and industrial activities in California's Central Valley and San Francisco Bay Area. Collaboration started in 2006 with the National Park Service with regard to air pollution generated by wildland fires including modeling the transport of pollutants generated in the mountains into the human-dominated valley. These research efforts will assist both the land managers and state and local air pollution regulators balance the need to restore fire to forest ecosystems with human health concerns and other sources of air pollutants.

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Effects of experimentally elevated N input on foliage element concentrations, tree increment and vitality in a Norway spruce stand, Gårdsjön, Sweden over an eleven–year period

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The effect of elevated anthropogenic nitrogen (N) on nutrient concentration, tree growth and vitality was studied by increasing the ambient throughfall from 11 kg N ha^{-1} yr^{-1} to approximately 51 kg ha^{-1} yr^{-1} in a 0.52 ha coniferous forest catchment. A solution of NH_4NO_3 was sprinkled below the tree canopy fortnightly in proportion to ambient throughfall. In an adjacent catchment, ambient N input to the forest soil was excluded by means of a roof beneath the tree canopy. The mean age of the forest was 104 years (1990). Nutrient concentrations in needle and litter and N flux in litter were measured prior to and over an 11-year-period following the start of the N addition in 1991.

A response to elevated N input was first observed in > 2 year old needles the fourth year of treatment (1994). In needle litter an increase was observed in 1995, whereas elevated N concentrations in current year needles was found in 1997. In the N exclusion catchment, a decrease in needle N concentration of all age classes was first observed in 1993. Apart from somewhat lower Mg concentration in needles from the N addition as well as from the N exclusion catchments, altered N input did not affect the concentration of major nutrients in needles over the 11-year period.

The C/N ratio in litter from the N addition and the control catchment decreased from 53 to 34 and from 55 to 48, respectively, between 1991 and 2001. The increased N concentration resulted in an increased total flux of N in litter. The total biomass flux of litter was not affected by elevated N input.

Generally, the basal area increment was declining in all the three catchments due to the age of the forest stands. The decline in the N addition plot was smaller relative to the control and N exclusion plots, indicating a positive growth response to the elevated N input. The N pool in standing biomass increased in both the control and the N addition catchment, with the highest increase observed in the N addition catchment. The elevated N input did not influence the forest health expressed as crown density and crown discoloration.

In conclusion, the N concentration in older year needles seem to be a better indicator of ecosystem N status and ecosystem response to elevated N input compared to current year needles.

Urbanization and atmospheric deposition:
use of bioindicators in determining patterns of land use change

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Land use changes accompanying urbanization disrupt ecosystem patterns and processes, and serve as precursors to ecosystem degradation allowing other environmental stressors to follow. Anthropogenic-induced factors contributing to these modifications include pollutant deposition, urban heat island effects, altered hydrology, and modified disturbance regimes. As such, forest ecosystems in urban and rapidly developing areas typically differ structurally and functionally from those in rural areas as a result of increased human presence. The purpose of this study was to determine differences in nutrient status and pollution loads in varying degrees of land use types. It is hypothesized that the effects of land use change and air pollutant exposure to forest ecosystems are revealed in bioindicators of ecosystem function, which can provide an indication of effects on forest biogeochemistry. The objectives of this study were to 1) to obtain lichen data for information about exposure that has occurred locally within the recent past, 2) utilize soil sample data for broader spatial coverage, 3) to use tree core data for historical records, and 4) to survey foliar injury to examine the potential impact of regional pollutant exposure. For this study we examined elemental concentrations in lichens, soils, and tree cores from thirty-six 0.05-hectare circular plots distributed along an urban-to-rural gradient near Columbus, Georgia. Samples were analyzed using inductively coupled plasma spectrometry (ICP) to obtain macronutrient and trace metal levels in each of these materials. Foliar injury was surveyed on known sensitive species within or near each plot. All of these data were then analyzed using ANOVA to discern differences in foliar injury, trace metal accumulation, and nutrient status between land use types. Preliminary results indicate that lichens appear to provide the most consistent results regarding potential differences in atmospheric deposition of pollutants among land use types. Lead, zinc, nitrogen, carbon, and sulfur concentrations were all highest at urban sites compared with developing and rural locations. In addition, C:N ratios were significantly lower for lichens collected from urban locations. In a fifty-year (1955-2005) age-based analysis of tree cores using ten-year increments, no discernable trends were observed regarding heavy metals and tree age.

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Atmospheric deposition and N status of German beech (*Fagus sylvatica*) forest

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The deposition situation of 1,800 forest monitoring sites in Germany for the year 1989 could be explained by four factors (three, excluding sea-salt impact) with the help of a factor analysis. The factors were grouped into 5 deposition types with typical compounds and regional patterns. The results of the correlation analysis between N deposition components and parameters describing the N status of 51 beech forests revealed that the human induced increase of N input into forest ecosystems significantly influences important ecosystem parameters. However, not all of the observed effects can be interpreted as cause and effect relationships because of the lack of detailed data, e.g. on soil solution and especially time series, but there are some clear trends.

A significant impact of N deposition on low buffered beech forests could be detected. High N depositions correspond with higher amounts of organic matter, higher C and N stocks in the organic layer as well as increased C/N ratios. Beech trees on sites with low Nt deposition have significant lower N contents in their leaves. These findings indicate a higher N saturation of low buffered beech forest sites due to high N depositions.

The study revealed a strong demand for time series data on intensive monitoring plots in beech forests. The findings should be further evaluated taking into account the trend towards declining deposition rates. Efforts should be strengthened to model atmospheric deposition – both site specific and on large scales.

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Session VIII

Influence of Air Pollution and Climate Change on Genetics, Adaptation and Succession

(David Karnosky, Chair)

Isoprene synthase and isoprene emission in aspen are inhibited more by elevated O_3 than elevated CO_2 in FACE conditions

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Biogenic emission by trees has a crucial role in the oxidizing potential of the atmosphere. In particular, isoprene oxidation leads to the formation of tropospheric ozone and other secondary pollutants. Isoprene is emitted in large amounts especially by poplars, aspen, oaks and eucalyptus trees. It is expected that changes in the composition of the atmosphere can influence the emission rate of isoprene and consequently have a strong effect on the atmospheric composition itself.

We investigated the isoprene synthase gene and the isoprene synthase protein level in aspen trees exposed to elevated O_3 and/or elevated CO_2 in open field at the AspenFACE experimental site located in northern Wisconsin. Isoprene synthase is the enzyme responsible of the formation of isoprene. Moreover we measured the isoprene emission rate from the leaves under the different treatments.

We found that elevated O_3 inhibited isoprene synthase gene expression and the amount of isoprene synthase protein in the leaves more than elevated CO_2. The inhibition was even stronger on the isoprene emission rate. Also, aspen clones with different O_3 sensitivity showed different levels of inhibition under elevated O_3 conditions.

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Impacts of elevated atmospheric CO_2 and O_3 on paper birch (*Betula papyrifera*) reproductive fitness**

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Atmospheric CO_2 and tropospheric O_3 are rising in many regions of the world. Little is known about how these two commonly co-occurring gases will affect reproductive fitness of important forest tree species. Here, we report on the long-term effects of CO_2 and O_3 for paper birch seedlings exposed for nearly their entire life history at the Aspen FACE (Free Air Carbon Dioxide Enrichment) site in Rhinelander, WI. Elevated CO_2 increased both male and female flower production while elevated O_3 increased female flower production compared to trees in control rings. Interestingly, very little flowering has yet occurred in combined treatment. Elevated CO_2 had significant positive effect on birch catkins size, weight and germination success rate (elevated CO_2 increased germination rate of birch by 109% compared to ambient CO_2 concentrations, decreased seedling mortality by 73%, increased seed weight by 17%, increased root length by 59% and root-to-shoot ratio was significantly decreased, all at three weeks after germination) while the opposite was true of elevated O_3 (elevated O_3 decreased the germination rate of birch by 62%, decreased seed weight by 25% and increased root length by 15%). Under elevated CO_2 plant dry mass increased by 9% and 78% at the end of 3 weeks and 14 weeks, respectively. Also, the root and shoot length as well as the biomass of the seedlings were increased for seeds produced under elevated CO_2 while the reverse was true for seedlings from seeds produced under the elevated O_3. Similar trends in treatment differences were observed in seed characteristics, germination and seedling development for seeds collected in both 2004 and 2005. Our results suggest that elevated CO_2 and O_3 can dramatically affect flowering and seed production and seed quality of paper birch, affecting reproductive fitness of this species.

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Impacts of elevated ozone and increased nitrogen on Finnish aspen and hybrid aspen clones

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Potted saplings of two Finnish aspen (*P. tremula*) and eight hybrid aspen (*Populus tremula* x *P. tremuloides*) clones were exposed to ambient ozone (control treatment) and 1,5 x ambient ozone (elevated-ozone treatment; equivalent to predicted near-future concentration in Finland) and two levels of nitrogen supply for two growing seasons at an open-air exposure field in Kuopio, Finland.

Ozone had a significant effect on dry mass of roots, shoot/root ratio and radial growth. Ozone decreased root dry mass and radial growth and increased shoot/root ratio in both nitrogen treatments. There was a significant decrease of height growth by ozone in low N trees but in high N trees, ozone increased height growth (O_3 x N interaction). Nitrogen addition increased stem and root dry mass and radial growth in both ambient and elevated O_3 concentrations. Ozone decreased photosynthesis, especially early in the growing season, whereas nitrogen did not have an effect on photosynthesis. Nitrogen increased photosynthesis later in the growing season but the positive effect of nitrogen addition was smaller in ozone treated plants. Ozone decreased and nitrogen increased F_v/F_m later in the growing season.

The clones were clustered into groups according to the impacts of ozone and nitrogen on different growth parameters. The Finnish aspen clones and four hybrid aspen clones were clustered in the group showing reduced growth in elevated ozone. In the ozone tolerant group, clone 193 showed increased growth in elevated ozone and added nitrogen. In the ozone sensitive group, clone 218 showed decreased growth in elevated ozone and no growth enhancement due to nitrogen addition. As there is clear intraspecific variation in ozone sensitivity in aspen and hybrid aspen, we want to further study which characteristics are important in determining ozone sensitivity or tolerance. We have e.g. found increased levels of flavonoid compounds in the leaves of ozone treated plants of the tolerant clone, where they could be acting as antioxidants against reactive oxygen species due to ozone attack.

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Industrial barrens: extreme habitats created by non-ferrous metallurgy

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Industrial barrens are bleak open landscapes evolved mostly in forested areas due to deposition of airborne pollutants, with only small patches of vegetation surrounded by bare land. These extreme environments appeared as a by-product of human activities about a century ago. The review aims at comparative analysis of information available from 26 industrial barrens worldwide; this analysis, in particular, allowed to identify factors and conditions that are necessary and sufficient for the development of industrial barrens. Vast majority of industrial barrens is associated with non-ferrous smelters, located predominantly in mountainous or hilly landscapes. Development of industrial barrens starts from gradual decline of vegetation due to severe pollution impact accompanied by other human-induced disturbances (primarily clearcutting) and is usually concluded by a fire, facilitated by accumulation of woody debris. Since vegetation recovery is hampered by soil toxicity due to extreme contamination by heavy metals, soils remain bare and suffer from erosion. In spite of general reduction in biodiversity, industrial barrens still support a variety of life, including regionally rare and endangered species, as well as populations that have evolved specific adaptations to the harsh and toxic environment. Industrial barrens offer unique opportunities for conducting 'basic' ecological research, in particular for testing some general theories in an evolutionary novel stressful environment; some of them deserve conservation for scientific and educational purposes.

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Northern deciduous trees are prone to ozone stress

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Atmospheric ozone is the most important oxidant affecting the forest ecosystems in the global scale. The forests have a critical part in national carbon budget especially in Nordic countries, where the forest ecosystems covers up to 70% of the land surface. In large areas of Finland, aspen and birch forestry offer the greatest potential for mitigate the climate change. However, our recent open-field experiments have indicated that these species are very susceptible to environmental stress factors such as ozone, but there is a large variation in tolerance among the genotypes. In this presentation we demonstrate shifts in the birch leaf metabolome and proteome after ozone exposure in realistic open-field conditions, and attempt to relate these changes with growth responses of sensitive and tolerant birch clones. Altogether 339 metabolites were quantified by HPLC-DAD and GC-MS analyses. The main ozone caused changes in birch metabolome included increases in quercetin-phenolic compounds and compounds related to leaf cuticular wax formation and decreases in compounds related to carbohydrate metabolism, some triterpenoids, as well as fatty acid and phytol derivatives. Changes in proteome were analyzed by 2D gel electrophoresis, combined with MS identification. In protein analyses, more than 900 protein spots were reproducibly detected by 2 D gel electrophoresis, and 13 proteins of them were significantly affected by ozone. For example, nucleoside diphosphate kinase (NDP kinase) was highly up-regulated, indicating a possible down-regulation of the accumulation of ROS and protection against ozone. The principal component analysis of metabolome dataset confirmed that the genotype caused most of the variance of metabolite concentrations, while ozone concentration was the second principal component explaining the shifts in leaf metabolites. This study indicated that in addition to economic impact, ecological functions of northern birch stands are subjected to changes at increasing ozone concentrations via alterations in leaf chemical properties. Needs for further experiments on interactive effects of warming and ozone on aspen and birch trees will be discussed.

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Interactive effects of elevated ozone and springtime frost on growth and physiology of birch (*Betula pendula)* in the field conditions

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According to global climate change predictions there is an increasing risk of concurrent exposure to elevated ozone concentrations and springtime frost in forest trees, especially in northern hemisphere. Silver birch is the most important commercial deciduous forest tree in Scandinavia and susceptible to elevated ozone concentrations, but there is a large variation in tolerance among genotypes. Co-occurring ozone enhancement may disturb the recovery from acute frost occurrence in birch as it has been indicated in our earlier chamber experiments. We have accomplished an experiment, where interactive effects of elevated ozone and springtime frost on growth and physiology of Silver birch were studied in field conditions using the same genotypes that showed different responses to ozone and frost stress in previous chamber experiments. Our experiment was conducted in free-air ozone enrichment (FACE) area at the Research Garden of University of Kuopio, where the seedlings were divided into four control (ambient air) and four ozone (1,5 x ambient) blocks in June 2003. Half of the seedlings were exposed to springtime frost in May 2004 after the bud burst. Plants were measured for timing of bud burst, visible ozone injuries, gas exchange and photosynthesis-related responses, as well as growth and carbon allocation. The main findings of this study were that the recovery of net photosynthesis from acute frost treatment was not complete during the subsequent three weeks, which led to significant growth reductions, and that reduced net photosynthesis after the frost was partly a result of impaired light capture due to loss of pigments. However, the reductions in pigment concentrations were greatest in ozone treated seedlings, and concomitant frost treatment tended to extenuate the effect of ozone on pigments and quantum yield of PS II. The effects of ozone on net photosynthesis were very variable and highly genotype-specific.

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Effects of temperature regimes on gene regulation in Norway spruce as indicated by DNA methylation

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In order to monitor gene regulation in trees, different sets of experiments were studied. Firstly, the proportions of 5-methylcytosine were assessed in total DNA extracts of Norway spruce (*Picea abies* (L.) Karst.) in response to elevated heat treatments. A standard treatment of eight week old seedlings almost doubled the proportion of methylated cytosine in the shoots but not in the roots whereas the three week old seedlings did not respond.

Secondly, full sib families from two independent pair-crosses performed both inside and outside a greenhouse express significant differences in the total methylation levels. Seedlings from seeds produced in the warm environment had higher levels of 5-methylcytosine than their full sibs from the outside control. Norway spruce seedlings seem to have a memory of the temperature experienced during embryogenesis that affect the timing of bud set.

Thirdly, we were able to demonstrate that differences in methylation were also expressed in two contrasting provenances: the lowland provenance sample had higher levels of methylation than the sample from high elevation. Finally, our data indicate that de-methylation occurs from embryo to seedling during germination, and that de-methylation is more pronounced in the provenance sample from high elevation. There was no evidence for a similar demethylation effect in *Arabidopsis thaliana*.

For the present, we assume that DNA methylation may be a part of a molecular memory mechanism that regulates genes involved in the control of adaptive traits in Norway spruce. The question of inherited vs. acquired resistance is furthermore raised and its practical consequences are outlined.

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