Review

Forests under climate change and air pollution: Gaps in understanding and future directions for research

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ABSTRACT

Forests in Europe face significant changes in climate, which in interaction with air quality changes, may significantly affect forest productivity, stand composition and carbon sequestration in both vegetation and soils. Identified knowledge gaps and research needs include: (i) interaction between changes in air quality (trace gas concentrations), climate and other site factors on forest ecosystem response, (ii) significance of biotic processes in system response, (iii) tools for mechanistic and diagnostic understanding and upscaling, and (iv) the need for unifying modelling and empirical research for synthesis. This position paper highlights the above focuses, including the global dimension of air pollution as part of climate change and the need for knowledge transfer to enable reliable risk assessment. A new type of research site in forest ecosystems ("supersites") will be conducive to addressing these gaps by enabling integration of experimentation and modelling within the soil-plant-atmosphere interface, as well as further model development.

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1. Introduction

Forest ecosystems are ecologically crucial, covering 30% of land area of Earth (FAO, 2006). Globally, forests store more than 80% of all terrestrial aboveground carbon (C) and more than 70% of all soil organic C (Dixon et al., 1994). Overall forests are currently global C sinks, whereas croplands are sources because of the more frequent soil disturbance associated with agricultural practices (Luyssaert et al., 2008; Schulze et al., 2009). Whether forests will remain C sinks will be determined by changes in photosynthesis, plant respiration and soil respiration, affecting the net ecosystem C flux. Such processes are strongly affected by changes in: (i) air quality,

comprising nitrogen (N) deposition (e.g. Nadelhoffer et al., 1999), ozone (O_3) exposure (e.g. Sitch et al., 2007), atmospheric carbon dioxide (CO_2) concentration (e.g. Friedlingstein et al., 1995) and aerosols/fine particulates (Mercado et al., 2009), (ii) climate warming (e.g. Myneni et al., 1997) with effects on water availability (e.g. Wamelink et al., 2009) and (iii) soil acidity and availability of non-N nutrients (Poorter and Nagel, 2000; Wamelink et al., 2009; De Vries and Posch, 2010).

These drivers affect C sequestration in both above and below ground biomass in forest ecosystems. Insight into the multi-factorial influences on air quality and climate change is crucial to provide a robust evidence base to policy makers. Such influences arise from the combustion of fossil energy resources and land-use changes (i.e. clear-cutting and forest burning), altogether releasing CO_2, nitrogen oxides (NO_x) and other climate-relevant trace gases. Emissions from forests add to those from intense agricultural practices, specifically

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ammonia (NH$_3$; IPCC, 2007) and methane (CH$_4$) from livestock (IPCC, 2007). In addition, natural emissions of volatile organic compounds (VOCs) from vegetation increase the mixture of reactants in the atmosphere (Laothawornkitkul et al., 2009). As trace gases accumulate, their reactivity may increase, if insolation is enhanced as an effect of atmospheric warming. Under high irradiance, some reactants become precursors to the formation of secondary pollutants, such as O$_3$ (Stockwell et al., 1997). With O$_3$ concentrations well above the pre-industrial levels (Vingarzan, 2004), and given the recent decrease in sulphur emissions in Europe and North America (−74% from 1990 to 2008; EEA, 2010; Smith et al., 2010), O$_3$ is regarded as the air pollutant potentially most detrimental to vegetation (Matyssek and Sandermann, 2003; Paoletti et al., 2007; Fowler et al., 2008; Wittig et al., 2007, 2009). On these grounds, forests currently face significant pressures from climate change and air pollution.

Until recently, dynamic global vegetation models predicted an increase in global productivity and terrestrial C sequestration in response to shifts in climate and CO$_2$ concentration (e.g. Cramer et al., 2001, 2004). These studies have been criticized for overestimating the potential carbon-climate feedback because C accumulation may be constrained by nutrients, particularly N (Hungate et al., 2003; Thornton et al., 2007), and by the negative impacts of elevated O$_3$ exposure (e.g. Grams et al., 1999, 2007; Karnosky et al., 2003, 2007; Wittig et al., 2009). Limitation by ozone may become substantial at the global scale by the end of this century (Vingarzan, 2004; Dentener et al., 2006; Sitch et al., 2007; Pretzsch et al., 2010), with significant consequences for radiative forcing in the atmosphere by elevated CO$_2$. Relationships of this kind vividly demonstrate air pollution is an intrinsic component of global change (Fowler et al., 2008), although awareness of this has only increased recently (Keating et al., 2004; Matyssek et al., 2010a).

The COST Action FP0903 was recently initiated to further integrate research on "Climate Change and Forest Mitigation and Adaptation in a Polluted Environment" (MAFor). The rationale of COST actions is to explore the state of knowledge within research fields and to initiate research cooperation. Hence, MAFor aims to (i) increase the understanding of the state and potential of forest mitigation and adaptation to climate change in a polluted environment, and (ii) reconcile experimental, process-oriented analyses and long-term monitoring with applied modelling to induce novel and integrative field research to enable risk upscaling to the ecosystem level and beyond (http://cost-fp0903.ipp.cnr.it/). At the inaugural conference in Rome/Italy, 5–7 October 2010, five knowledge gaps and associated research needs were identified in relation to MAFor:

- Focus I: Interactions between trace gases, climate change and vegetation
- Focus II: Significance of biotic processes in forest ecosystem response
- Focus III: Tools for mechanistic and diagnostic understanding and risk upscaling
- Focus IV: Unifying modelling and empirical research
- Focus V: Global dimension of air pollution as part of climate change

This position paper highlights these knowledge gaps and what research is needed to address them. The evaluation focuses on the possibilities to achieve such clarification through research at "supersites" (Fischer et al., 2011). These sites are to be established in a range of forest ecosystems to determine their responses to air pollution and climate change impacts. The rationale for such supersites will briefly be introduced in the following *prior to* featuring the above focuses.

2. The rationale of "supersites" in forest ecosystem research

The concept of "supersites" acknowledges the scientific need for process-based assessments of present and future ecological risks for forests. It requires the integration of research communities with operational expertises on monitoring and/or research networks and process and large-scale modelling (Fischer et al., 2011). Supersites have to be established as highly instrumented research infrastructures in forest ecosystems and to become components of transcontinental collaboration networks in order to integrate existing monitoring and research sites of current trans-national co-operations. Ecosystem-level monitoring and mechanistic modelling should be combined with long-term cause/effect-based experimentation under prevalent, ecologically relevant stand conditions across the major European forest types, striving for stable national and EU-level funding. Harmonisation of existing and newly elaborated databases is a necessity for consolidating knowledge about climate change and air pollution impact on forest ecosystem C sequestration and storage, soil chemistry and water budgets. Mechanistic ecosystem understanding is the ultimate aim, along with knowledge transfer to predictive modelling and tool development for reliable risk assessment. To this end, forest–atmosphere interactions will be emphasized, including CO$_2$ exchange, VOC and biogenic aerosol turnover, O$_3$ formation and uptake, and N deposition related to forest tree and ecosystem performance. A pre-requisite will be joint concept development and continuing scientific communication between experimentalists, monitoring experts and modellers. Fig. 1 visualizes the kind of cooperation and parameter assessment that supersites will need.

3. Focus I: interactions between trace gases, climate change and vegetation

The complex response of trees and forest ecosystems to environmental impacts can create both positive and negative feedbacks in C budgets (Arneth et al., 2010b). N availability strongly affects both the net primary productivity (NPP) of vegetation and the decay of dead organic material. In most pristine temperate and boreal terrestrial ecosystems, N constrains production and biogeochemical fluxes (Vitousek and Howarth, 1991), thus N deposition leads to elevated productivity (Aber et al., 1998; Matson et al., 2002; Pregitzer et al., 2008; De Vries et al., 2008, 2009). This tendency, associated with increased water-use efficiency, is reinforced by elevated CO$_2$ (Cao et al., 2010; Drake and Gonzàlez-Meler, 1997).
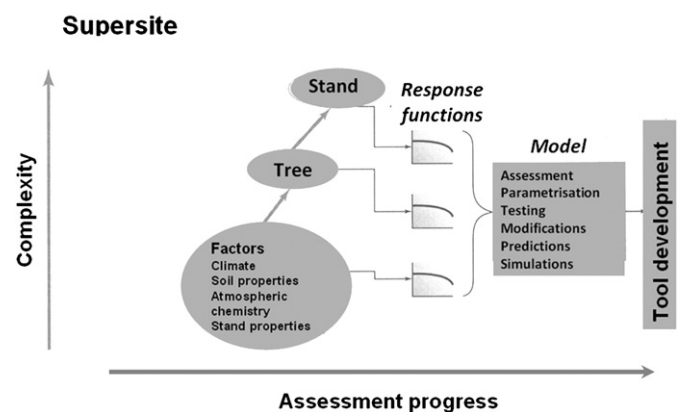

Fig. 1. "Supersite" – a new kind of research site in forest ecosystems, integrating experimentation within the soil-plant-atmosphere interface and model development (adapted from Matyssek et al., 1995; see Fischer et al., 2011 for details).

Plants may even promote NPP by the formation of N and sulphur (S) containing biogenic aerosols (fine particulates) that increase diffuse radiation favouring photosynthesis (Mercado et al., 2009). Another effect of climate warming is longer growing seasons (provided risks of early and late frosts stay low; Hasenauer and Monserud, 1997; Gao et al., 2009) and temperature-driven N mineralization (Bonan and van Cleve, 1992; Reichstein et al., 2000). Conversely, increased temperature increases the evaporative pressure on plants (Rebetez and Dobbertin, 2004), which eventually induces drought and stomatal closure (Zweifel et al., 2007). The latter response not only limits photosynthesis (Körner, 2003), but also O_3 influx (Matyssek et al., 2006), reducing primary productivity and the terrestrial C sink (Sitch et al., 2007). It is uncertain whether drought-induced limitation of photosynthesis upon stomatal closure is the "smaller evil" to trees in comparison with injury caused by otherwise unhindered O_3 influx (Karnosky et al., 2003; Matyssek et al., 2006). Growth can also be inhibited by high N deposition (e.g. Boxman et al., 1998), which in addition may increase the susceptibility to early/late frosts, although reports are contradictory (e.g. Perkins et al., 2000; Jönsson, 2000; Fløistad, 2002).

Interactions among trace gases are also complex. NO_x and VOCs are crucial in driving the net productivity of O_3, having lowering or enhancing capacities depending on the atmospheric circumstances. The ambiguity is high in the case of VOCs, which can be released in high amounts from vegetation and, therefore, may significantly contribute to O_3 formation. Conversely, vegetation provides a sink for O_3 deposition and scavenging (Calfapietra et al., 2009; Fowler et al., 2009). Reliable information on pollutant absorption is, however scarce. In this context, millions of hectares of short-rotation plantations with poplar and eucalypt species around the world (in particular, in Asia) known for high biogenic VOC emissions (Wiedinmyer et al., 2006), need investigation. Hence, vegetation itself must increasingly be understood as a driver of gas interactions and determinant of the atmospheric O_3 balance.

One particular issue is the process-based understanding of the link between precursor dynamics and O_3 regimes. Precursor emissions have declined in Europe (CO by −58%, non-methane VOCs by −51% and NO_x by −39% within the EU from 1990 to 2008; EEA, 2010), but background O_3 concentrations have continued to increase (at +0.9% per year at European remote stations since the 1970s; Vingarzan, 2004). The frequency of high instantaneous O_3 peaks varies from year to year but shows no clear trend (EEA, 2011). Mechanistic clarification is required, for which local, regional and global-scale models of atmospheric chemistry and transport are needed (see Focus IV). The potential for VOC emissions appears to be crucial for tree species selection in forestry, as the temperature dependence of such emissions is governed by positive feedbacks between vegetation, atmosphere and climate change conditions.

The emission of the greenhouse gas CH_4 from vegetation is stimulated in species and site-specific ways by high temperature and ultraviolet radiation (Bruhn et al., 2009; Vigano et al., 2008). *In situ* studies over coniferous forest ecosystems have so far not been able to quantify CH_4 emissions (Bowling et al., 2009; Smeets et al., 2009).

To address the knowledge gaps identified in Focus I it is proposed that supersites will provide research platforms (supported by tower and/or free-air fumigation experiments) for clarifying:

- interactions between vegetation and CO_2, O_3 and N regimes under progressive climate warming and associated positive feedbacks,
- interactions between trace gases, including VOCs, as mechanistic grounds and determinants of the atmospheric aerosol formation, precursor dynamics and O_3 balance.

4. Focus II: significance of biotic processes in forest ecosystem response

Tree and ecosystem responses are influenced by biotic as well as abiotic factors. A pre-requisite for valuating system responsiveness is knowledge of pollutant uptake, which in the case of air pollution mainly occurs via stomata. Consequently, empirical clarification of stomatal conductance, its maximum level and regulation, is mandatory, irrespective of the pollutant under consideration, to warrant reliable risk scaling across trees, ecosystems and landscapes (Matyssek et al., 2008; Köstner et al., 2008; Wieser et al., 2008). Leaf-anatomical parameters (e.g. stomatal density, leaf compactness) can provide proxies of tree sensitivity for model development (Karlsson et al., 2007; Matyssek et al., 2008), but these approaches have largely been neglected (see Focus III and IV).

The concurrent impact of elevated CO_2 and O_3 may result in complex tree responses. Elevated CO_2 may ameliorate adverse O_3 effects, in particular, on C sink strength, whereas enhanced O_3 may neutralize stimulation in productivity under high CO_2 (Karnosky et al., 2003; Matyssek et al., 2010a). How the response will be affected by climate change is even less well understood (Calfapietra et al., 2010). Plant responses to both gases also depends on N availability (Körner, 2006; Maurer and Matyssek, 1997; Magnani et al., 2007). Drought interplays with CO_2/O_3 interactions, as it curtails both C sink strength and O_3 uptake into plants via stomatal closure (Matyssek et al., 2006a). Aboveground O_3 impacts on plants indirectly affects belowground processes, by influencing fine-root production, mycorrhization and soil respiration through alterations in resource allocation and phytohormonal relationships (Nikolova et al., 2010; Matyssek et al., 2010b). As a consequence, water, nutrient and C storage capacities of soils (the dominant C pool in forest ecosystems) become affected so that changes may in turn alter their sensitivities to climate change and air pollution. Consequently, edaphic factors such as soil nutrition and moisture, as well as soil texture and chemistry (including soil C fractions), need to become part of risk analysis. It must not be overlooked, however, that key biotic determinants of responsiveness are internal factors such as the genotype and phenological and ontogenic stage of the trees.

Plant communities are crucial modifiers in system behaviour. Competitive interactions between plants, both above and belowground, can buffer or exacerbate the impacts of climate change and air pollution (Kozovits et al., 2005; Kubiske et al., 2007; Matyssek et al., 2010a,b). Other modifying interactions occur between plants and pathogens or consumers. Elevated N supply may increase the palatability of foliage leading to enhanced attractiveness to herbivores/pathogens (Herms and Mattson, 1992; Van Dijk et al., 1992; Flückiger and Braun, 1998). A substantial component of biotic interactions occur between plants and microrrhizae. Mycorrhizal plants can develop enhanced stress tolerance, as observed in defence against pathogens, which may be, similar to some pollutants, oxidative stressors (Matyssek and Sandermann, 2003; Matyssek et al., 2005). Chronic exposure to ozone may even harden trees against pathogenic infection (Luedemann et al., 2005; Bahnweg et al., 2005; Olbrich et al., 2010). It is apparent that competitive and mutualistic interactions with pathogens and beneficial micro-organisms belowground, are drivers of ecosystem C sequestration.

The ways in which biotic interactions determine tolerance and avoidance of environmental stress is a frontier in research and of relevance for risk assessment. O_3 stress avoidance is determined by stomatal regulation under biotic and abiotic influences which restricts O_3 uptake (i.e. the phytotoxically relevant O_3 dose) (Matyssek et al., 2007). Stress tolerance may be viewed as responsiveness per unit of O_3 uptake, reflecting the effective O_3

dose (Musselman et al., 2006; Matyssek et al., 2008). Clarification of abiotic and biotic impacts on C cycling and C sink formation in forest ecosystems is crucial for developing silvicultural practices that take account of climate change and air pollution effects. This is vital, if ecosystem services such as timber production, biodiversity conservation, water quality and recreation and aesthetic value are to be optimised. Mechanistic understanding is required on trade-offs between anthropogenic stress impact versus C pool formation in forest ecosystems.

To address the knowledge gaps identified in Focus II, it is proposed that supersites will enable measurement of:

- tree and ecosystem level pollutant uptake as determined by stomatal regulation and canopy-level diffusive conductance,
- interactions between elevated CO_2 and O_3 regimes in tree and ecosystem response (in particular, if operating free-air fumigation experiments at the sites; Karnosky et al., 2007; Calfapietra et al., 2009; Matyssek et al., 2010a,b),
- biotic influences on ecosystem response through genotypes, ontogeny and phenology of trees, as well as competitive, mutualistic and parasitic above and belowground interactions,
- abiotic and biotic impacts on C cycling and C sink formation in forest ecosystems in association with water and nutrient relations.

5. Focus III: tools for mechanistic and diagnostic understanding and risk upscaling

Mechanistic understanding as postulated by Focus II is a prerequisite for scaling findings on stress responsiveness across adjacent levels of biological organization. An important internal plant link is the one between the level of metabolic control (i.e. gene regulation and transcript level) and that of metabolic activity (i.e. biochemical and physiological processes) (Matyssek et al., 2005). This kind of research has been neglected dramatically, hence a synthetic understanding is lacking when studying plant responses to climate change and air pollution, although respective methodologies are available. High throughput capacities for transcript sequencing, proteomic analysis, and assessment of primary and secondary metabolites are waiting for rigorous employment in climate change and air pollution research. Questions include whether phospho-proteomics can be carried out in trees, if epigenetic effects should be considered and how outcomes can be integrated in modelling approaches (see Focus IV). In particular, molecular research needs to be linked to ecophysiological research, to understand the plasticity in tree response in mechanistic terms (Sandermann and Matyssek, 2004). Validation of laboratory and greenhouse studies is required at field sites (Matyssek et al., 2005, 2010a), in particular, in view of the metabolic regulation between above and belowground resource allocation and phloem loading and transport under scenarios inciting stress defence.

An underlying challenge is to strive for marker development across the plant-internal levels of spatio-temporal organisation (Sandermann and Matyssek, 2004). Regarding O_3 stress, crucial *parameters* to be considered are (i) stomatal conductance (Ashmore, 2004; Karlsson et al., 2004; Grünhage et al., 2004; Matyssek et al., 2007; Serengil et al., 2011), (ii) constitutive detoxification capacity (Plöchl et al., 2000), (iii) carboxylase ratio (ribulose bisphosphate carboxylase and phospho*enol*pyruvate carboxylase) during photosynthetic decline but increasing catabolism/respiration and (iv) capacity for antioxidant regeneration (in tight relation to the redox power by NADPH as provided through catabolic pathways) (Dizengremel et al., 2008, 2009; see Fig. 2 for details). Scaling must extend to the ecosystem level and beyond
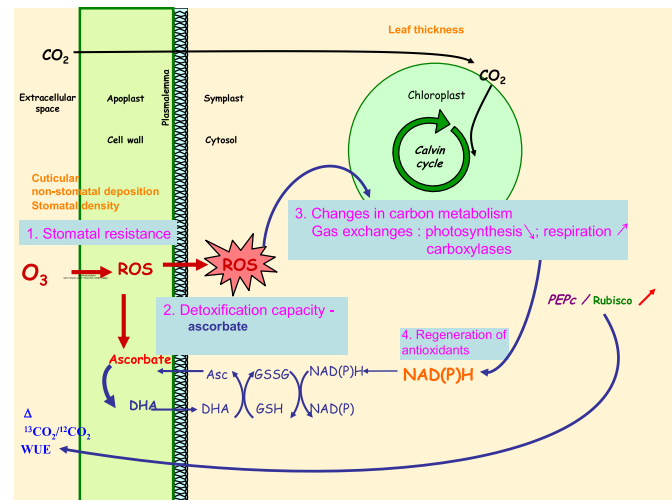

Fig. 2. Parameters determining whole-tree O_3 sensitivity, (1) stomatal conductance, (2) constitutive detoxification capacity, (3) ratio between carboxylases (rubisco and PEPcase), and (4) antioxidant regeneration as based on redox power (i.e. NADPH availability; see text) provided through catabolic pathways. High apoplastic ascorbate levels for counteracting O_3-caused toxicity (Castagna and Ranieri, 2009) need to be regenerated by the cell metabolism, controlling the "effective O_3 flux" upon O_3 uptake through stomata (Matyssek et al., 2008; Musselman et al., 2006). Regeneration of ascorbate requires the reducing power of NADPH (Dizengremel et al., 2008, 2009), while O_3 impact on photosynthesis is typically associated with decreasing and increasing activities of rubisco and PEPc, respectively (Saurer et al., 1995; Renaut et al., 2009). Related stimulation of catabolic pathways keeps NADPH high (Dizengremel et al., 2009). High PEPc/rubisco activity ratios lower the discrimination of ^{13}C versus ^{12}C in CO_2 fixation, which interferes with the discrimination by stomatal regulation, so that the resulting δ^{13}C signature may be reflected in biomass formation (Saurer et al., 1995; Dizengremel et al., 2008). Decline in photosynthesis at increasing demand for detoxification and repair will curtail growth (Wieser and Matyssek, 2007) and may affect whole-tree C allocation (Matyssek et al., 2010a,b).

(Sandermann and Matyssek, 2004). The goal must be to understand system behaviour along transitions from controlled laboratory to relevant field conditions, from juvenile to mature plants (being most important for trees), from short-term changes to long-term effects, and from the individual plant towards the ecosystem level, the region and the globe (Fig. 3; Matyssek et al., 2005; Wieser et al., 2008).

To address the knowledge gaps identified in Focus III it is proposed that supersites will enable investigation of:

- mechanistic grounds for ecosystem responsiveness, comprising the molecular level of metabolic control and the biochemical and physiological process levels of metabolic activity, and for process scaling across spatio-temporal levels of biological organization.
- biological markers of environmental impact across the different levels of spatio-temporal organisation, for promoting tool development for differential stress diagnosis and process-based risk assessment and upscaling to the ecosystem level and beyond (in particular, if operating free-air fumigation experiments at the sites) (Karnosky et al., 2007; Calfapietra et al., 2009; Matyssek et al., 2010a,b).

6. Focus IV: unifying modelling and empirical research

Model development is needed to assess long-term and large-scale forest ecosystem development in response to environmental changes. In this context, dynamic global vegetation models (DGVMs) are needed that quantify the interacting impacts of changes in air quality (trace gas concentrations) and climate change on ecosystem
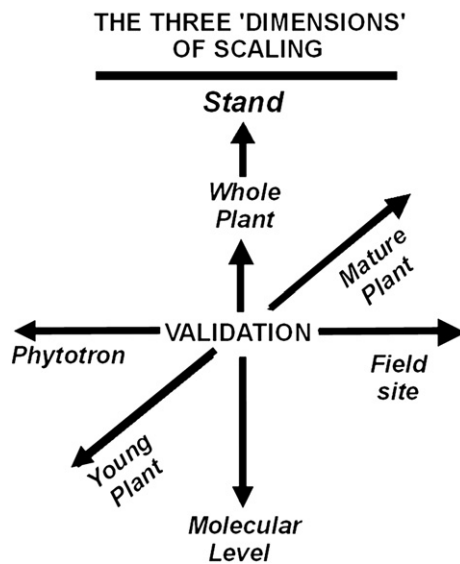
THE THREE 'DIMENSIONS' OF SCALING

Stand

Whole Plant

Mature Plant

VALIDATION

Phytotron ← → **Field site**

Young Plant

Molecular Level

Fig. 3. The "*Three Dimensions of Scaling*", after Matyssek (2001), comprise process transitions between (1) the molecular and stand level, (2) ontogenetic stages and (3) growth conditions (controlled chamber/laboratory versus ecologically relevant site conditions). Dimension (1) may be extended to ecosystem, landscape and hemisphere (cf. Wieser et al., 2008), intrinsically linked with temporal scaling from short towards long-term scopes at spatially high hierarchical levels (Sandermann and Matyssek, 2004).

productivity on a regional to continental scale. DGVMs were originally developed to highlight the feedbacks between the terrestrial C cycle and the climate system by assessing shifts in vegetation and the associated exchange of energy, water and C through impacts on plant growth, competition, mortality, and changes in ecosystem structure (Cramer et al., 2001; Friedlingstein et al., 2006). As C accumulation may be constrained by nutrients, particularly N (Hungate et al., 2003; Thornton et al., 2007), interactions of CO_2, climate and N availability have recently been included in several DGVM's such as ORganising Carbon and Hydrology In Dynamic EcosystEms (ORCHIDEE) (Zaehle and Friend, 2010; Zaehle et al., 2010) and the Community Land Model (CLM) (Thornton et al., 2009). Another impact often neglected in DGVMs is that of O_3 exposure and its interaction with effects of CO_2, climate and N availability. Sitch et al. (2007) recently modified a DGVM to include the effect of O_3 deposition on photosynthesis, accounting for interactions between O_3 and CO_2 on the land-C sink through stomatal closure. Their results showed that the uptake of O_3 by the canopy has notable detrimental effects on photosynthesis, which may affect the terrestrial C sink (Sitch et al., 2007). DGVMs have also currently been expanded by including the atmosphere-biosphere exchange of non-CO_2 trace gases, such as biogenic VOCs (Arneth et al., 2010a).

Regional to continental modelling tools depend in their precision on the availability and quality of underlying data for parameterization and validation. These data are scarce for models focusing on forest ecosystems under climate change and air pollution. This holds true, in particular, for effects of enhanced O_3 concentrations, with model parameterizations still being based on agricultural rather than adult-tree and ecosystem-level data. Validation mainly relies on findings from pioneer tree species in plantations, such as poplar (Sitch et al., 2007). This implies that both the quantification of the O_3 impact at the detailed process level and the integration of effects at the level of the entire tree are difficult to achieve for mature trees. This also holds true for the empirical information on the interacting effects of trace gases (O_3, CO_2), nutrients and climatic parameters (temperature, water availability), as experiments generally focus on

two or three interactions only. In order to improve the models, there is no other way than augmenting empirical databases through innovative experimentation under forest site conditions (Calfapietra et al., 2009). This need is exemplified by the models of biogenic VOC emissions that do not consider the interactions with O_3 concentrations (e.g. Arneth et al., 2008), although feedbacks are known to exist between these gaseous constituents (Lerdau, 2007; Calfapietra et al., 2009). Similarly, deposition models should include these and other chemical interactions that are relevant to the deposition process.

An important limitation of complex models is that modelling rationales often presume smooth equilibrium system development, whereas the environment will continue to change during the coming decades. Models often ignore the fact that long-term changes are affected by episodic perturbation that causes system development to depart from equilibrium states. To account for this, probability algorithms are sometimes implemented into modelling, covering those factors which are most likely to cause episodic impact and discontinuities in system behaviour (Seidl et al., 2011). While this may appear to produce more realistic results, the predictions also become more uncertain. It should be kept in mind, however, that most quantitative models, in combination with experimental studies, are geared towards understanding ecosystem dynamics rather than prediction of future developments under different scenarios of global change.

For meeting the requirement of augmenting databases suitable for model development and validation, research projects must include, as a pre-requisite, an intense interaction between experimentalists and modellers (Matyssek et al., 2005). This means that experimentation and modelling must be conceived as a single functional unit, necessitating a continuous communication on both experimental design and model development, to generate synergistic insights beyond the current state of knowledge. The main objective of such joint endeavours must be the mechanistic understanding of the system response to climate change and air pollution. With more advanced process understanding, empirical research can be reconciled with long-term monitoring and upscaling modelling, and the robustness of risk assessment methods can be enhanced. Robustness does not necessarily mean a maximum complexity in modelling, but an optimized description of key processes built upon empirical knowledge.

The mechanistic understanding of air pollution on plant-physiological processes needs to be transferred to the models that describe the atmosphere-biosphere exchange of pollutants and the related forest productivity response. This involves integration over a wide range of hierarchical levels, from basic physiological processes to the whole-tree C balance (Mohren et al., 1992), and a further upscaling to the landscape scale. Such development is crucial for the risk assessment methodologies employed for policy-making within UNECE (United Nations Economic Commission for Europe; Mills, 2010) and the EU. This especially involves the DO_3SE model (Deposition of O_3 and Stomatal Exchange; Emberson et al., 2000) and the atmospheric chemistry–transport model of EMEP (European Monitoring and Evaluation Programme; Simpson et al., 2007) that are used to assess the exposure of forests to phytotoxic O_3 uptake and N deposition. Future research needs of these models and of DGVMs include the interactions between CO_2, O_3, N availability and climate, while detoxification capacity should be integrated into O_3 risk indices. Robust and validated models are needed for policy-oriented applications (Tuovinen et al., 2009). Validation of models is possible using atmosphere-forest flux measurements (Tuovinen et al., 2004), and is especially important for the stomatal O_3 uptake that controls both the deposition rates and the potential for detrimental effects (Fowler et al., 2009).

In summary, understanding the role of climate change and air pollution in mechanistic terms within risk assessment requires

modelling of biogeochemistry and functional biodiversity processes. This new kind of modelling will be helpful to unify scientific communities focusing on air pollution and on climate change, which typically have operated with little communication in the past.

To address the knowledge gaps identified in Focus IV it is proposed that supersites will enable:

- combined experimental research and model development, generating synergistic insights beyond the current state of knowledge on interactions between CO_2, O_3, N availability and climate on forest growth, element cycling and soil carbon sequestration.
- validation of models with data about the combined impacts of air quality and climate on forest ecosystem development.

7. Focus V: global dimension of air pollution as part of climate change

The global dimension of climate change has long been acknowledged. However, in the case of air pollution, which undoubtedly is a component of climate change (see Introduction), such a global perception has only developed since the early nineties (e.g. Keating et al., 2004). The change in perception has mainly occurred because tropospheric O_3 is enhanced above pre-industrial levels (Vingarzan, 2004) and enhanced N deposition levels have been observed in large parts of Asia (e.g. Dentener et al., 2006). Both O_3 and N have been considered as regional pollutants in European-scale air pollution abatement as opposed to the global perspective of climate change. This difference in public/political awareness and scientific perception favoured the persistence of separated research communities, i.e. dealing either with air pollution or climate change (see Focus IV).

In the meantime, plumes with high O_3 levels have been demonstrated to be transported at the transcontinental scale both across Eurasia and within North America, and in addition, across the northern hemisphere from North America to Europe (Newell and Evans, 2000; Wang et al., 2009; Davis et al., 2010). This is one argument for regarding enhanced O_3 levels as a global factor. Another is the predicted further increase of O_3 regimes across major regions around the world, including upcoming "hot spots" in the southern hemisphere (Muramoto et al., 2003; Zunckel et al., 2004). A further argument is that tropospheric ozone is a powerful greenhouse gas. Even though ozone is a short-lived pollutant that tends to form local hotspots of high concentration, ozone radiative effects are global and long-lasting (Moore, 2009). What is needed, therefore, are global research networks on air pollution and climate change with (i) O_3 as the key pollutant with its highly adverse potential effect on vegetation as part of climate change and (ii) N, being the primary nutrient limiting ecosystem productivity (Zaehle and Friend, 2010; Zaehle et al., 2010) thus partly offsetting the adverse effects of O_3 on productivity, but bearing a risk for C sink strength as well (see Focus IV). Model simulations suggest a tremendous decline globally in gross primary productivity of forest systems, fostering radiative forcing of the atmosphere, due to O_3 (Sitch et al., 2007), although parameterization and validation are debatable (see Focus IV). The postulated networks need to ensure effect monitoring and reconciliation of research concepts and modelling methodologies at the global scale (Arneth et al., 2010b).

To address the knowledge gaps identified in Focus V it is proposed that supersites will:

- be extended beyond the European scale, in particular, to upcoming new "hot spots" in climate change and air pollution predicted for East Asia and the southern hemisphere.

8. Conclusions and perspectives

Focuses I–V have detailed research needs and given perspectives towards consolidating risk assessment. Knowledge gaps include the interactions between trace gases and other site factors, consolidating mechanistic and ecologically relevant understanding of system response for grounding diagnostic tools, integrating modelling and empirical research, as well as conceiving air pollution as a global component of climate change. One fundamental starting point for integrative research that would cover this broad range of knowledge gaps in empirical evidence and associated modelling would be the introduction of a new kind of research sites in forest ecosystems, i.e. so-called "supersites" (Fischer et al., 2011). These would integrate soil science, plant-physiological and atmospheric studies within experiments specifically designed to support both the development of new models and the validation of existing ones. Key features would be the integration of physical, chemical and biological processes at the soil-vegetation-atmosphere interface. The research needs identified in each focus indicate how supersites can be conducive to overcoming present gaps in knowledge about air pollution and climate change effects on forest ecosystems.

In summary, the future directions for research are to:

- unify air pollution and climate change research for forest ecosystems,
- collaborate on "supersites" as highly instrumented research infrastructures in forest ecosystems which are components of transcontinental collaboration networks.
- strengthen communication between experimentalists, monitoring experts and modellers.
- promote predictive modelling on mechanistic grounds towards tool development for reliable risk assessment.

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