PROJECT INFORMATION

Project title: **PROFILE - Predicting Ozone Fluxes, Impacts, and critical Levels on European forests**

Project ID: 107

Contact person: Marcus Schaub (marcus.schaub@wsl.ch)

PROJECT DESCRIPTION

Draft Proposal_vrs4

Authors:

M. Schaub[1,2,]*, M. Haeni[1,2], S. Etzold[1,2], P. Waldner[1,2], R. Zweifel[1,2], A. Gessler[1,2], A. Rigling[1,2], M. Rebetez[1,2], E. Solly[1,2], M. Ferretti[3], E. Gottardini[4], V. Calatayud[5], P. Büker[6], L. Emberson[6], D. Simpson[7,8], ICP Forests Experts[x] ..., ForClim[y], CASTANEA[z], ..., M. Cailleret[1, 2]

[1]Swiss Federal Research Institute WSL; [2]SwissForestsLab; [3]TerraData environmetrics; [4]Research and Innovation Centre, Fondazione Edmund Mach (FEM); [5]Fundación CEAM, Paterna 46980, Spain; [6]Stockholm Environment Institute, University of York; [7]EMEP MSC-W, Norwegian Meteorological Institute; [8]Department of Earth & Space Sciences, Chalmers University of Technology; [x]contributing ICPF EPs; [y]contributing ForClim colleagues; [z]contributing CASTANEA colleagues, ...

**Corresponding author: marcus.schaub@wsl.ch*

Summary

Tropospheric ozone (O_3) is considered to be more damaging to vegetation than any other air pollutant. Public concerns, evidence from research, and increasing scientific knowledge are all driving widespread discussions on ozone risk assessment and dose-response relationships for European forests. The ICP Forests network comprises over 200 long-term monitoring plots where ozone concentrations have been measured since 2000, in parallel to vegetation parameters such as tree

growth. This study aims to determine ozone fluxes for assessing ozone related effects on selected endpoints and deriving and validating ozone critical levels for forests by (i) coupling the DO$_3$SE model with the forest succession ("gap") model ForClim and by (ii) developing an "Ozone-version" of CASTANEA that can simulate various impacts of ozone on tree functions by implementing new functions from DO$_3$SE. Data sources from various networks will be explored and applied for model calibration, application and validation. The expected results will be an important contribution the objectives of the UNECE WG on Effects.

Introduction

Tropospheric ozone (O$_3$) is considered to be more damaging to vegetation than any other air pollutant and levels and patterns of global exposure to ozone may change dramatically over the next 50 years, impacting global warming, air quality, and ecosystem function (Ainsworth *et al.*, 2012).

Globally, ozone is estimated to reduce biomass production of northern hemisphere forest trees by ca. 7% at current ozone levels (Wittig *et al.*, 2009). Others argue that ozone affects adult trees significantly, but effects on stem growth are hard to prove and difficult to correlate with the primary sites of ozone damage at the leaf level (Deckmyn *et al.*, 2007; Bussotti & Ferretti, 2009).

Braun *et al.* (2014) applied epidemiological analyses of stem increment data from *Fagus sylvatica* L. and *Picea abies* Karst. in Swiss forest plots and found 19.5%, 6.6.% and 11.0% growth reduction for deciduous, coniferous and for all forested areas, respectively, based on annual ozone stomatal uptake during 1991-2011. Wang *et al.* (2016) assessed the impact of ozone on forest composition and ecosystem dynamics with an individual-based gap model that includes basic physiology as well as species-specific metabolic properties. They conclude that elevated ozone leads to no reduction of forest productivity and carbon stock and that ozone may not diminish forest carbon sequestration capacity.

To simulate ozone effects in a mechanistic way, at a level relevant to forest stand growth, Deckmyn *et al.* (2007) developed a simple ozone damage and repair model (CASIROZ model) that can be implemented into mechanistic photosynthesis and growth models. This ozone sub-model was used in the ANAFORE forest model to simulate gas exchange, growth, and allocation. Preliminary simulations for the Kranzberg beech site (Matyssek *et al.*, 2010) show that, although ozone effects on yearly growth are variable and therefore insignificant when measured in the field, they could become significant at longer timescales (above 5 years, 5% reduction in growth). The results further helped to understand ozone effects by distinguishing defense from damage and repair (see Kolb *et al.*, 1997).

Interactions between forests and atmospheric pollutants are a crucial component of Earth System Science, but as shown above the impact of ozone on the productivity of forest ecosystems is discussed controversial and is not yet well understood. Not only growth reduction is inconsistent but also photosynthetic responses are not straightforward. While numerous studies have found significant ozone effects on photosynthesis on the leaf level (Novak *et al*., 2005, 2007), with increasing spatial perspective, the evidence of harmful ozone effects is fading (Leuzinger *et al.*, 2011). Deckmyn *et al.* (2007) offers a possible explanation for the discrepancy between the significant effects on photosynthesis, and the minor effects on growth. They argue that such a discrepancy may be the result of the strong competition and slow growth of forest trees, and the importance of stored carbon (by buffering effects on carbon gain). While the approach by Wang *et al.*, (2016) is intriguing, the main weakness of the study seems to be the classification of species into ozone-resistant, intermediate and sensitive species - based on literature. For example, they cited (Schaub *et al.*, 2003), a seedling study, but missed the complementing study by (Schaub *et al.*, 2005) on mature canopy trees, which would have been much more appropriate but does not show as clear results as the seedling study. Furthermore, a classification for ozone sensitivity is always tricky and may be biased.

Furthermore, ozone is involved in N- and C-cycles in a complex way, but the impacts on vegetation within the mix of climate, other pollutants and biotic stressors are difficult to quantify, especially for forests (Simpson *et al.*, 2014) and climate conditions and atmospheric deposition are highly inter correlated with counteracting or interacting effects, leading to complex interrelationships, which are difficult to disentangle and to predict (Etzold *et al*., in prep.)

At the latest UNECE Critical Levels Workshop in Deganway (June 2016), it has been highlighted that there is a large potential in exploiting data from the European-wide ICP Forests monitoring network to determine ozone fluxes for assessing ozone related effects on selected endpoints and deriving and validating ozone critical levels for forests.

It is thus our aim to estimate forest productivity on selected UNECE ICP Forests plots retrospectively and in future to determine the impact of (i) climatic conditions and (ii) ozone exposure and the interactions between both factors. The proposed study aims at integrating different national (LWF, Sanasilva, LFI, TreeNet, IAP) and international (ICP Forests, ICP Vegetation, EMEP) networks, use measured (LWF, TreeNet, Sanasilva, LFI, IAP, Kranzberg, ECMWF, NCEI) as well as modeled (MeteoSwiss, MeteoTest, EMEP) data sources and will be conducted under the auspice of the SwissForestLab.

Approach

We argue that the (simulated) impacts of ozone on short- and long-term forest productivity and dynamics strongly vary according to the site-specific properties of the forest (i.e., structure and composition; e.g., not considered in Braun *et al*., 2014) and to the local environmental conditions (mainly soil properties and climate). To account for the complex interrelationships and multifactorial growth effects under varying environmental and stand conditions, and to consider for the feedbacks between ozone deposition on the leaves and the development of the stand canopy (via ozone-induced changes in tree growth and stand LAI), we propose a new approach that combines process-based models simulating physiological processes at organ and tree scales, and demographic processes at stand scale. Our project will be divided into two main components:

1. **"Hybrid approach"** (i.e. not fully mechanistic)

Here, we aim at simulating the long-term (i.e., multi-decadal) impacts of ozone on forest productivity and dynamics by coupling the model DO$_3$SE with the forest succession ("gap") model ForClim.

The DO$_3$SE (Deposition of O$_3$ for Stomatal Exchange) model has been developed to estimate ozone deposition and stomatal flux for various vegetation types across Europe. DO$_3$SE provides a receptor specific, critical phytotoxic ozone dose (PODy; accumulated ozone stomatal fluxes above a threshold y) based on the stomatal diffuse conductance. The stomatal flux is estimated at an hourly time step by using the multiplicative model from Jarvis (1976) modified by Emberson *et al*. (2000), and is a function of the species-specific maximal conductance, leaf phenology, light availability, air temperature and VPD, and soil moisture. DO$_3$SE was continuously developed and tested during the last decades with a specific focus on a better consideration of the impact of drought on stomatal conductance (e.g., Büker *et al*., 2012; De Marco *et al*., 2016).

ForClim is a climate-sensitive gap model that simulates the dynamics of temperate forests over a wide range of environmental conditions (Bugmann 1996). The establishment, growth, and mortality of trees are simulated on small areas ('patches'), based on a minimum of ecological assumptions to capture the influence of the main climate and ecological processes on long-term forest dynamics (e.g., drought, frost, soil nitrogen availability, competition for light). In the last years, the model has been subjected to several modifications, especially to better simulate annual diameter increment in managed stands (Rasche *et al*., 2012; Mina *et al*., 2015). In its initial version, ForClim included a submodel for the turnover of soil organic matter, and thus could simulate temporal changes in soil nitrogen availability based on litter decomposition (Bugmann 1996). However, considering the difficulty to assess parameter values from this submodel in the field (e.g., lignin/nitrogen ratio of the litter decay), and the slight dependency of simulated growth to nitrogen availability for species other than *Acer sp.*, we will not consider for temporal modifications in soil nitrogen concentration (through uptake and deposition).

Model development

DO_3SE and ForClim will be coupled via the reduction in individual tree growth caused by ozone, and stand height and LAI as described in Figure 1.

For each year of simulation, DO_3SE will simulate PODy based on hourly ozone concentration- and climate data and on canopy main characteristics, i.e., stand-level maximum height and Leaf Area Index (**step 1**). Based on the simulated annual PODy and PODy-growth response functions that are empirically derived (Büker *et al*., 2015; Schaub *et al*. (in prep using Swiss Level II plots for 2009-2014), a reduction in annual biomass increment caused by ozone is predicted (hereafter O_3GF for O_3-growth reducing factor; **step2**). Size-specific response functions will be used when available (i.e., by differentiating mature *vs*. juvenile trees). The annual diameter increment (Dinc) of every cohort is then calculated by ForClim as a function of species-specific maximum growth rate which is reduced by several 'growth reduction factors' related to the level of ozone (O_3GF), crown characteristics (crown length growth factor; CLGF), light availability (available light growth factor; ALGF), soil nitrogen availability (soil nitrogen growth factor; SNGF), and soil water availability (soil moisture growth factor; SMGF). Equations are available in Mina *et al*. (2015; **step 3**). Finally, the annual change in stand-level maximum height and LAI – used as input of DO_3SE – are calculated by ForClim based on Dinc and species-specific allometric relationships (Moore 1989; ref LAI; **step 4**).

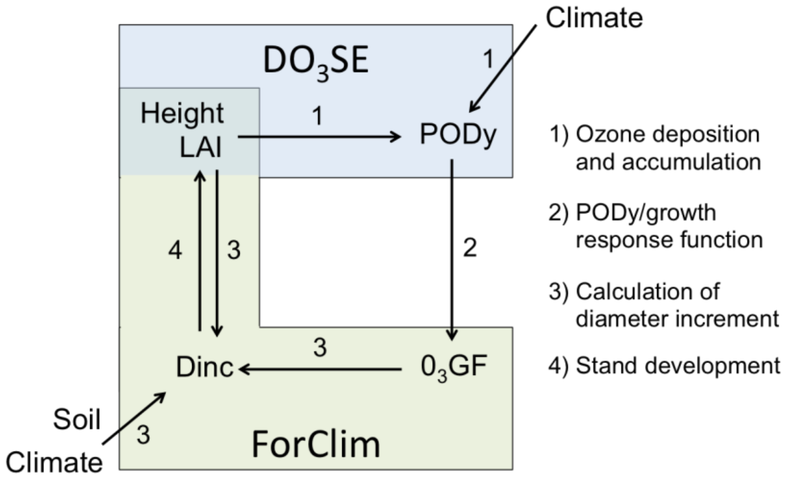

Figure 1. Coupling between ForClim and DO_3SE via PODy/growth response function and stand

development.

Model calibration

Both DO_3SE and ForClim models are already independently calibrated, such as the PODy-growth response functions that will be used (derived from the literature; see above). We do not attempt to modify any parameter estimates.

Model validation

The coupled model will be validated at stand scale on monospecific forests (even-aged?) by comparing the observed and simulated temporal development of the basal area of stands from selected (i) ICP Forests Level II and (ii) NFI plots. The model will be initialized based on forest inventory data (and LAI data) at the first inventory and run until the last inventory (e.g., from 2000 to 2015 for ICP Level II forest plots). Climate, soil, and ozone data will be provided by various networks such as LWF, MeteoTest, MeteoSchweiz (for Switzerland) and ICP Forests Level II plots, The European Centre for Medium-Range Weather Forecasts (ECMWF)[1], NOAA's National Centers for Environmental Information (NCEI)[2], and EMEP for EU plots.

Model application

Runs into the future under different (i) climate change, (ii) management, and (iii) ozone concentration scenarios. Different approaches will be used to detect the respective importance of each of these components on the projected variability in forest productivity and dynamics, from sensitivity analysis to variance decomposition analysis including mixed-effects models. As null hypothesis, we will consider that effect of ozone on forest productivity and dynamics is negligible in comparison to the effect of climate change. Note that this analysis can be done even if there is a systematic under- (or over-) estimation of stand growth.

2. "Mechanistic approach"

CASTANEA is a mechanistic model simulating the carbon-, water- and energy-balances in forest stands. Tree structure is represented by a combination of five functional compartments: leaves, stems, branches, coarse and fine roots (Dufrêne *et al.*, 2005). In its initial version, CASTANEA was restricted to the simulation of even-aged stands ('averaged-tree model' that did not take into

---

[1] Url: http://www.ecmwf.int/en/research/climate-reanalysis/era-20c

account the variability between trees). However, it has recently been coupled with a stand structure model to consider for the intra-site differences in growth rates related to tree size and competition intensity (Guillemot *et al*., 2014). This development allows for the prediction of structure dynamics in uneven-aged stands and for an explicit simulation of forest management.

CASTANEA and DO_3SE will not be directly coupled such as for the hybrid approach. Here, we rather prefer at developing an "Ozone-version" of CASTANEA that can simulate various impacts of ozone on tree functions by implementing new functions from DO_3SE or other process-based models. Note that feedbacks between ozone deposition and forest structure will be also considered via ozone-induced changes in tree functions, growth, and in stand characteristics (e.g., LAI).

We selected the CASTANEA model for several reasons:

First, it accurately describes the main physiological processes at organ and tree scales (photosynthesis, respiration, hydraulics, carbon allocation, wood and leaf phenology etc.), but also at stand scale (stand growth, carbon and water cycles, litter decomposition etc.). It should allow for an explicit and mechanistic simulation of the feedbacks between ozone deposition and ozone impacts, e.g., through (i) ozone-induced changes in photosynthetic capacities or [and] in leaf phenology, and (ii) the impact of the modifications in canopy structure on ozone deposition. In addition, as the physical processes within the canopy and the soil (e.g., diffusion, interception) are explicitly simulated by considering multiple layers, the model should correctly predict the effect of light and water availability on stomatal conductance and thus on ozone uptake. An accurate quantification of tree water status is especially key to quantify PODy (De Marco *et al*., 2016). Finally, thanks to the calculation of different ecological variables (e.g., transpiration, NEE, tree diameter increment), a large variety of data with different spatial and temporal resolutions can be used to validate the model, from sap-flux measurements to ring-with data, including stand-scale eddy-covariance measurements.

Second, if other physiological process-based models can simulate the feedbacks between ozone deposition and forest structure and functions, such models were usually developed for a single species growing in one single site (e.g., Deckmyn *et al.*, 2007 and Matyssek *et al*., 2010 with the ANAFORE model), or for plant functional types over a large grid with low spatial resolution (>10 km grid; e.g., Sitch *et al.*, 2007; Anav *et al.*, 2012; Lombardozzi *et al*., 2015; De Marco *et al*., 2016; Franz *et al*., 2016 or Yue *et al*., 2016 with Earth System models). Thus, the predictions and projections that result from both types of modeling studies can be either hardly extrapolated in space, or they lack of precision at stand and regional scales. For instance, Earth System models cannot consider for the

---

[2] Url: https://gis.ncdc.noaa.gov/geoportal/catalog/search/resource/details.page?id=gov.noaa.ncdc:C00532

large variability in the sensitivity to ozone deposition among tree species (Büker *et al*., 2015). In this context, stand-scale process-based models that have been calibrated and validated for several species and sites seem to be highly appropriate to simulate forest functions and development at regional or country scales. Although the spatial resolution is quite limited (generally less than 1 ha), they can be applied in a high number of stands with various environmental conditions, forest compositions and structures. It generally eases the interpretation of the results, and leads to more realistic model predictions and projections as it considers for the current diversity in forest types and for potential management impacts. On these aspects, the CASTANEA model has been validated for several European tree species in different sites (*Fagus sylvatica*, *Picea abies*, *Quercus robur*, *Pinus sylvestris, Pinus pinaster*, *Quercus ilex*; Davi *et al*., 2005, 2006; Delpierre *et al*., 2009; Davi and Cailleret 2017) and was successfully applied at country scale to predict species distribution (Cheaib *et al*., 2012) or stand productivity in managed forests (Guillemot *et al*., 2014).

Third, the impact of soil nitrogen concentration and tree carbon budget is considered through relationships between leaf and stem nitrogen concentration and photosynthetic and respiration rates. An improved version of the nitrogen submodel is currently under development (Delpierre in prep.) and will explicitly link the nitrogen, carbon, and water cycles. It would allow for an accurate assessment of the nitrogen cycle at ecosystem scale, and especially for the quantification of the interactive effects of nitrogen deposition, ozone, and climate change on tree functions.

Finally, as we aim at predicting and projecting the impact of ozone pollution on forest productivity, a key component of the modeling approach lies in the simulation of individual tree growth. Considering that tree growth is driven by both carbon sources and sinks (Körner 2015; Delpierre *et al*., 2015), the allocation of carbon to wood growth should depend on (i) the quantity of carbon available through photosynthesis and the reserves, and on (ii) the cambial activity which is driven by the environment (mainly temperature and water availability). In this context, CASTANEA includes a state-of-the-art carbon allocation scheme (Davi *et al*., 2009; Guillemot *et al*., 2015), which especially allows for an accurate simulation of the inter-annual variability in tree growth (Davi and Cailleret 2017). Moreover, thanks to the recent coupling with a stand structure model, the new model version distributes the carbon allocated to wood growth (in gC) to the different trees depending on their sizes (Guillemot *et al*., 2014), and thus can simulate an intra-site variability in individual tree growth.

Model development

As described in Figure 2, the ozone module of CASTANEA will be connected to several physiological processes:

a) Quantification of stomatal cumulative ozone uptake (or phytotoxic ozone dose), and of non-stomatal ozone destruction based on atmospheric ozone concentration measurements, canopy structure, and stomatal conductance. DO_3SE equations will be used (Emberson *et al.*, 2000; Simpson *et al.*, 2012).

b) Stomatal conductance. We aim at simulating the impact of ozone on stomatal closure (and sluggishness?) by modifying the Ball & Berry equation currently implemented in CASTANEA. Some examples are available in Fares *et al.* (2013) and Hoshika *et al.* (2015).

c) Photosynthetic capacities. Ozone damages the photosynthetic apparatus resulting in a decline in net photosynthesis (Wittig *et al.*, 2007). This phytotoxic effect will be considered either by reducing the maximum carboxylation rate (V_{cmax}) based on relationships with cumulative ozone uptake that were empirically derived (e.g., Lombardozzi *et al.*, 2012 on tulip poplar), or by reducing net photosynthesis (A_n) using damage relationships such as in Sitch *et al.* (2007), Lombardozzi *et al.* (2015), or Franz *et al.* (2016). Species-specific relationships will be preferred if available in the literature (e.g., from Wittig *et al.*, 2007 and/or Lombardozzi *et al.*, 2013).

d) Carbon allocation to defense mechanisms against ozone damage to compensate for the decrease in photosynthesis. Depending on which formula we will use to simulate the effect of ozone on photosynthesis, a detoxification function can be implemented to reduce the accumulated uptake of ozone. In that case, the quantity of carbon allocated to these defenses will also be estimated, for instance *via* an increase in dark respiration rates (Fusaro *et al.*, 2016). Some modeling examples are available in Deckmyn *et al.* (2007) or Franz *et al.* (2016).

e) Leaf phenology module to simulate the impact of ozone on leaf senescence (Jolivet *et al.*, 2016) for the species in which such effect has been observed (e.g., slight effect for beech; Gielen *et al.*, 2007).

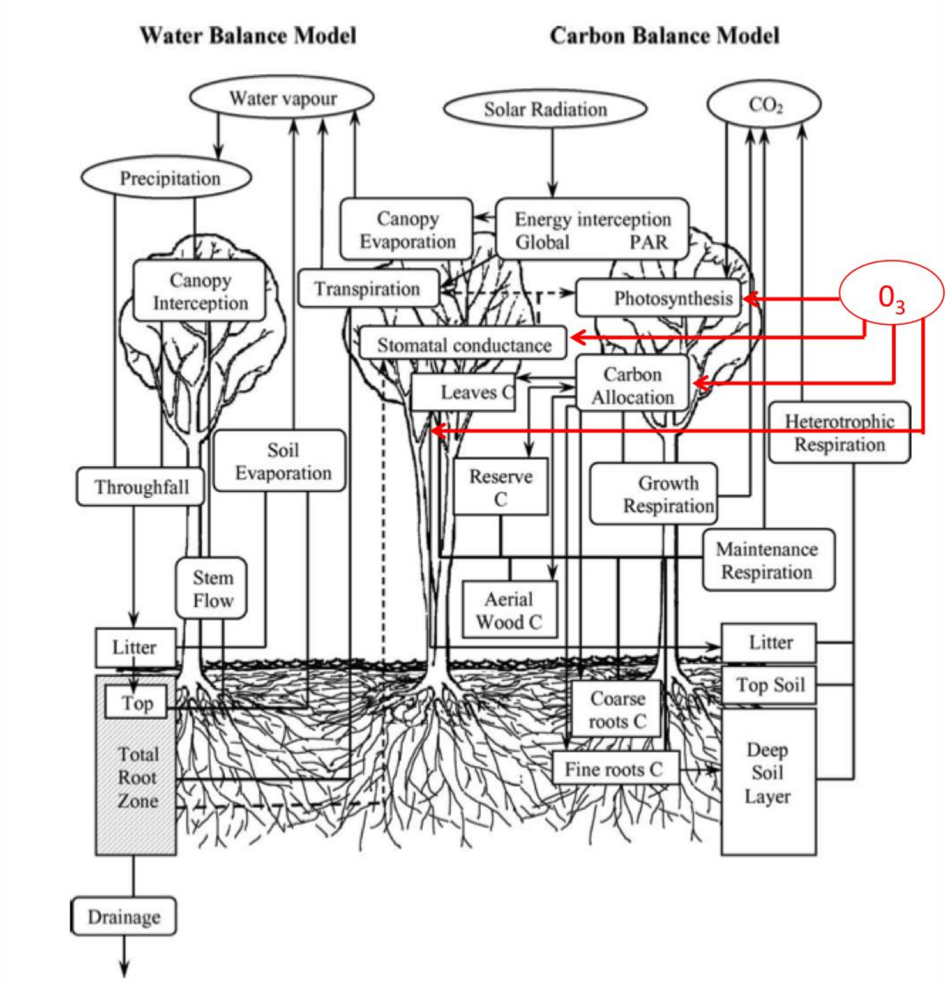

Figure 2. Main physiological processes and pools considered in CASTANEA, including the ones we intend to implement (in red).

Model calibration

The functions not yet implemented in CASTANEA nor DO$_3$SE will be based on literature analysis using data from adult trees as much as possible. Depending on recent DO$_3$SE developments, we may have to include some equations to simulate the diffusion of ozone between the different layers of the canopy (e.g., using one single layer may lead to an overestimation of ozone uptake). In addition, new analytical harvesting interventions will be implemented if needed (for model validation).

Model validation

Model validation will be performed using data with various spatial and temporal resolutions from several sources and networks, including ICP Forests, NFIs, EMEP, ECMWF, NCEI and CASIROZ (Matyssek *et al.*, 2010). Annual and multi-annual tree growth data, based on ring-width and forest inventory measurements are available from ICP Forests and NFIs (LWF, Sanasilva, IAP and LFI for Switzerland) and would allow for model validation at inter-annual scale. Sap-flow data and observations of leaf and wood phenology from the TreeNet network and the Kranzberg forest site will also be used to validate model predictions at intra-annual resolution. We will also derive PODy – Relative biomass curves and compare them with the ones empirically derived by Büker *et al*., 2015.

Model application

Runs into the future under different (i) climate change, (ii) management, (iii) CO2 concentration, (iv) nitrogen deposition, and (v) ozone concentration scenarios. Different approaches will be used to detect the respective importance of each of these components on the projected variability in stand productivity and other functions (e.g., carbon storage; from sensitivity analysis to variance decomposition analysis including mixed-effects models and multifactorial approaches. We especially aim at detecting differences among species (e.g., between deciduous and coniferous), and among sites (forest structure, soil and climatic conditions).

Expected output

The anticipated study will provide dose-response functions for selected tree species grown on long-term forest monitoring plots and will hence be an important contribution to the current discussions on critical levels.

Based on this ensemble of model runs, we will be able to detect environmental tipping points that would lead to a strong decrease in stand productivity (e.g., -50% in comparison to current conditions) or to forest dieback. This includes the determination of species-specific, site-specific, and climate change-specific ozone critical levels. The results will be published in scientific ISI journals, UNECE Reports and Policy Briefs. Furthermore, a collaboration with EEA is anticipated to disseminate our results via e.g. the EEA webpage on indicators[3].

---

[3] Url: http://www.eea.europa.eu/data-and-maps/indicators#c0=10&b_start=0

References

Ainsworth, E.A., Yendrek, C.R., Sitch, S., Collins, W.J. & Emberson, L.D. (2012) The effects of tropospheric ozone on net primary productivity and implications for climate change. *Annu Rev Plant Biol*, **63**, 637-61.

Anav, A., Menut, L., Khvorostyanov, D., & Viovy, N. (2012). A comparison of two canopy conductance parameterizations to quantify the interactions between surface ozone and vegetation over Europe. *Journal of Geophysical Research: Biogeosciences*, ***117***(G3).

Bircher, N., Cailleret, M., & Bugmann, H. (2015). The agony of choice: different empirical mortality models lead to sharply different future forest dynamics. *Ecological Applications*, ***25***, 1303-1318.

Braun, S., Schindler, C. & Rihm, B. (2014) Growth losses in Swiss forests caused by ozone: epidemiological data analysis of stem increment of Fagus sylvatica L. and Picea abies Karst. *Environ Pollut*, **192**, 129-38.

Büker, P., Feng, Z., Uddling, J., Briolat, A., Alonso, R., Braun, S., ... & Marzuoli, R. I. C. C. A. R. D. O. (2015). New flux based dose–response relationships for ozone for European forest tree species. *Environmental Pollution*, ***206***, 163-174.

Bugmann, H. K. (1996). A simplified forest model to study species composition along climate gradients. *Ecology*, ***77***, 2055-2074.

Bussotti, F. & Ferretti, M. (2009) Visible injury, crown condition, and growth responses of selected Italian forests in relation to ozone exposure. *Environ Pollut*, **157**, 1427-37.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., ... & Thuiller, W. (2012). Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology letters*, ***15***, 533-544.

Davi, H., & Cailleret, M. (2017). Assessing drought-driven mortality trees with physiological process-based models. *Agricultural and Forest Meteorology*, ***232***, 279-290.

Davi, H., Dufrêne, E., Granier, A., Le Dantec, V., Barbaroux, C., François, C., & Bréda, N. (2005). Modelling carbon and water cycles in a beech forest: Part II.: Validation of the main processes from organ to stand scale. *Ecological Modelling*, ***185***, 387-405.

Davi, H., Dufrêne, E., Francois, C., Le Maire, G., Loustau, D., Bosc, A., ... & Moors, E. (2006). Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. *Agricultural and Forest Meteorology*, ***141***, 35-56.

Deckmyn, G., Op de Beeck, M., Low, M., Then, C., Verbeeck, H., Wipfler, P. & Ceulemans, R. (2007) Modelling ozone effects on adult beech trees through simulation of defence, damage, and repair costs: Implementation of the CASIROZ ozone model in the ANAFORE forest model. *Plant Biol (Stuttg)*, **9**, 320-30.

Delpierre, N., Berveiller, D., Granda, E., & Dufrêne, E. (2015). Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. *New Phytologist*.

Delpierre, N., Soudani, K., Francois, C., Köstner, B., PONTAILLER, J. Y., Nikinmaa, E., ... & Grünwald, T. (2009). Exceptional carbon uptake in European forests during the warm spring of 2007: a data–model analysis. *Global Change Biology*, ***15***, 1455-1474.

De Marco, A., Sicard, P., Fares, S., Tuovinen, J. P., Anav, A., & Paoletti, E. (2016). Assessing the role of soil water limitation in determining the Phytotoxic Ozone Dose (PODY) thresholds. *Atmospheric Environment*.

Dufrêne, E., Davi, H., François, C., Le Maire, G., Le Dantec, V., & Granier, A. (2005). Modelling carbon and water cycles in a beech forest: Part I: Model description and uncertainty analysis on modelled NEE. *Ecological Modelling*, ***185***, 407-436.

Emberson, L. D., Ashmore, M. R., Cambridge, H. M., Simpson, D., & Tuovinen, J. P. (2000). Modelling stomatal ozone flux across Europe. *Environmental Pollution*, ***109***, 403-413.

Etzold et al. (in prep.) Impacts of site quality, air quality and climate on growth of European forest ecosystems.

Fares, S., Matteucci, G., Mugnozza, G. S., Morani, A., Calfapietra, C., Salvatori, E., ... & Loreto, F. (2013). Testing of models of stomatal ozone fluxes with field measurements in a mixed Mediterranean forest. *Atmospheric Environment*, ***67***, 242-251.

Franz, M., Simpson, D., Arneth, A., & Zaehle, S. Development and evaluation of an ozone deposition scheme for coupling to a terrestrial biosphere model. *Biogeosciences*, in press

Fusaro, L., Gerosa, G., Salvatori, E., Marzuoli, R., Monga, R., Kuzminsky, E., ... & Fares, S. (2016). Early and late adjustments of the photosynthetic traits and stomatal density in Quercus ilex L. grown in an ozone-enriched environment. *Plant Biology*, ***18***, 13-21.

Gielen, B., Löw, M., Deckmyn, G., Metzger, U., Franck, F., Heerdt, C., ... & Ceulemans, R. (2007). Chronic ozone exposure affects leaf senescence of adult beech trees: a chlorophyll fluorescence approach. *Journal of Experimental Botany*, ***58***, 785-795.

Guillemot, J., Delpierre, N., Vallet, P., François, C., Martin-StPaul, N. K., Soudani, K., ... & Dufrêne, E. (2014). Assessing the effects of management on forest growth across France: insights from a new functional–structural model. *Annals of botany*, ***114***, 779-793.

Guillemot, J., Martin-StPaul, N. K., Dufrêne, E., François, C., Soudani, K., Ourcival, J. M., & Delpierre, N. (2015). The dynamic of the annual carbon allocation to wood in European tree species is consistent with a combined source–sink limitation of growth: implications for modelling. *Biogeosciences*, ***12***, 2773-2790.

Hoshika, Y., Katata, G., Deushi, M., Watanabe, M., Koike, T., & Paoletti, E. (2015). Ozone-induced stomatal sluggishness changes carbon and water balance of temperate deciduous forests. *Scientific reports*, *5*.

Jarvis, P. G. (1976). The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, ***273***(927), 593-610.

Jolivet, Y., Bagard, M., Cabané, M., Vaultier, M. N., Gandin, A., Afif, D., ... & Le Thiec, D. (2016). Deciphering the ozone-induced changes in cellular processes: a prerequisite for ozone risk assessment at the tree and forest levels. *Annals of Forest Science*, 1-21.

Kolb, T.E., Fredericksen, T.S., Steiner, K.C. & Skelly, J.M. (1997) Issues in scaling tree size and age responses to ozone: A review. *Environmental Pollution*, **98**, 195-208.

Körner, C. (2015). Paradigm shift in plant growth control. *Current opinion in plant biology*, ***25***, 107-114.

Leuzinger, S., Luo, Y.Q., Beier, C., Dieleman, W., Vicca, S. & Korner, C. (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology & Evolution*, **26**, 236-241.

Lombardozzi, D., Levis, S., Bonan, G., Hess, P. G., & Sparks, J. P. (2015). The influence of chronic ozone exposure on global carbon and water cycles. *Journal of Climate*, ***28***, 292-305.

Lombardozzi, D., Sparks, J. P., Bonan, G., & Levis, S. (2012). Ozone exposure causes a decoupling of conductance and photosynthesis: implications for the Ball-Berry stomatal conductance model. *Oecologia*, ***169***, 651-659.

Lombardozzi, D., Sparks, J. P., & Bonan, G. (2013). Integrating O 3 influences on terrestrial processes: photosynthetic and stomatal response data available for regional and global modeling. *Biogeosciences*, ***10***, 6815-6831.

Matyssek, R., Wieser, G., Ceulemans, R., Rennenberg, H., Pretzsch, H., Haberer, K., Löw, M., Nunn, A.J., Werner, H., Wipfler, P., Oßwald, W., Nikolova, P., Hanke, D.E., Kraigher, H., Tausz, M., Bahnweg, G., Kitao, M., Dieler, J., Sandermann, H., Herbinger, K., Grebenc, T., Blumenröther, M., Deckmyn, G., Grams, T.E.E., Heerdt, C., Leuchner, M., Fabian, P. & Häberle, K.H. (2010) Enhanced ozone strongly reduces carbon sink strength of adult beech (Fagus sylvatica) – Resume from the free-air fumigation study at Kranzberg Forest. *Environmental Pollution*, **158**, 2527-2532.

Mina, M., Bugmann, H., Klopcic, M., & Cailleret, M. (2015). Accurate modeling of harvesting is key for projecting future forest dynamics: a case study in the Slovenian mountains. *Regional Environmental Change*, 1-16.

Novak K, Cherubini P, Saurer M, Fuhrer J, Skelly JM, Kräuchi N, **Schaub M** (2007) Ozone air pollution effects on tree-ring growth, delta13C, visible foliar injury and leaf gas exchange in three ozone-sensitive woody plant species. *Tree Physiology* 27(7):941-949.

Novak K, **Schaub M**, Fuhrer J, Skelly JM, Hug C, Landolt W, Bleuler P, Kräuchi N (2005) Seasonal trends in reduced leaf gas exchange and ozone-induced foliar injury in three ozone sensitive woody plant species. *Environmental Pollution* 136:33-45.

Rasche, L., Fahse, L., Zingg, A., & Bugmann, H. (2012). Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. *Ecological Modelling*, ***232***, 133-143.

San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds.)(2016) European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg.

Schaub, M., Skelly, J., Zhang, J., Ferdinand, J., Savage, J., Stevenson, R., Davis, D. & Steiner, K. (2005) Physiological and foliar symptom response in the crowns of Prunus serotina, Fraxinus americana and Acer rubrum canopy trees to ambient ozone under forest conditions. *Environmental Pollution*, **133**, 553-567.

Schaub, M., Skelly, J., Steiner, K., Davis, D., Pennypacker, S., Zhang, J., Ferdinand, J., Savage, J. & Stevenson, R. (2003) Physiological and foliar injury responses of Prunus serotina, Fraxinus americana, and Acer rubrum seedlings to varying soil moisture and ozone. *Environmental Pollution*, **124**, 307-320.

Simpson, D., Arneth, A., Mills, G., Solberg, S. & Uddling, J. (2014) Ozone — the persistent menace: interactions with the N cycle and climate change. *Current Opinion in Environmental Sustainability*, **9-10**, 9-19.

Simpson, D., Benedictow, A., Berge, H., Bergström, R., Emberson, L. D., Fagerli, H., ... & Jenkin, M. E. (2012). The EMEP MSC-W chemical transport model–technical description. *Atmospheric Chemistry and Physics*, ***12***(16), 7825-7865.

Sitch, S., Cox, P. M., Collins, W. J., & Huntingford, C. (2007). Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature*, ***448***(7155), 791-794.

Wang, B., Shugart, H.H., Shuman, J.K. & Lerdau, M.T. (2016) Forests and ozone: productivity, carbon storage, and feedbacks. *Sci Rep*, **6**, 22133.

Wittig, V. E., Ainsworth, E. A., & Long, S. P. (2007). To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant, cell & environment*, ***30***, 1150-1162.

Wittig, V.E., Ainsworth, E.A., Naidu, S.L., Karnosky, D.F. & Long, S.P. (2009) Quantifying the impact of current and future tropospheric ozone on tree biomass, growth, physiology and biochemistry: a quantitative meta-analysis. *Global Change Biology*, **15**, 396-424.

Yue, X., Keenan, T. F., Munger, W., & Unger, N. (2016). Limited effect of ozone reductions on the 20-year photosynthesis trend at Harvard forest. *Global Change Biology*.