



Universität für Bodenkultur Wien
University of Natural Resources
and Life Sciences, Vienna

Department of Forest and Soil Sciences

Institute of Silviculture

Supervisor: Univ.Prof. Dipl.-Ing. Dr. Hubert Hasenauer

**MANAGEMENT OF DYNAMIC FOREST FUNCTIONS BASED ON
CARBON, NITROGEN AND WATER CYCLES**

Dissertation

**to obtain the doctoral degree (Dr.nat.techn.) at the
University of Natural Resources and Life Sciences, Vienna**

Elisabeth Pötzelsberger

Vienna, March 2015

PREFACE

This thesis summarises as a 'cumulative dissertation' four separate journal articles covering my past research. In this thesis with the topic 'Management of dynamic forest functions based on carbon, nitrogen and water cycles' I introduce the reader to my dissertation topic (chapter 1), highlight the objectives of my work (chapter 2), present the relevant methods (chapter 3) and data (chapter 4), give an overview of the results of my studies (chapter 5), discuss what the implications of the results are and how this all blends to significant findings (chapter 6) and derive my conclusions (chapter 7). In this way, the framework paper gives a common structure to the individual articles and allows interpretation of the study results that goes beyond the scope of the individual papers. The relevant articles for my dissertation are named in the section LIST OF PEER REVIEWED PUBLICATIONS and are given in the APPENDIX. The format of the articles is as prescribed by the publishing journals.

This work shall be cited as appropriate for the purpose, either by the individual journal articles or as:

Pötzelsberger, E., 2015. Management of dynamic forest functions based on carbon, nitrogen and water cycles. Dr.nat.techn. dissertation, University of Natural Resources and Life Sciences, Vienna, pp. 85.

LIST OF PEER REVIEWED PUBLICATIONS

- I. Pötzelsberger, E., Hasenauer, H., 2015. Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests. *For. Ecol. Manage.* 338, 176–182.
- II. Pötzelsberger, E., Hasenauer, H., 2015. Forest–water dynamics within a mountainous catchment in Austria. *Nat. Hazards*. doi: 10.1007/s11069-015-1609-x
- III. Warren, J.M., Pötzelsberger, E., Wullschleger, S.D., Thornton, P.E., Hasenauer, H., Norby, R., 2011. Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂. *Ecohydrology* 4:196–210.
- IV. Pötzelsberger, E., Wolfslehner, B., Hasenauer, H., 2015. Climate change impacts on key forest functions of the Vienna Woods. *Eur. J. For. Res.* doi: 10.1007/s10342-015-0866-2

ACKNOWLEDGEMENTS

It is a long path to where one can eventually sit down and write the acknowledgements for a dissertation. Along the way I have met countless people who have helped me reach this point with both large or small contributions to my work and wellbeing. I want to sincerely thank all of them.

My gratitude goes to my colleagues at BOKU, who supported me with their scientific knowledge and good humour. Special thank goes to Dr. Stephan Pietsch for introducing me to the beauties and drawbacks of mechanistic ecosystem modelling, to Dr. Richard Petritsch and Dr. Christopher Thurnher, who always answered my technical questions and were there for some inspiring discussions, to Dr. Mario Klopff, who never failed to share his knowledge on silviculture and also some important lines of R-code. I would also like to thank DI. Dominik Thom, who inherited Mario's workplace and hence also his 'duties', Dr. Roland Köck for his training in vegetation analysis, Mag. Christian Quehenberger and Dr. Fritz Putzhuber for all their field work, Dr. Chris Eastaugh for knowing how to bring fun into a harsh PhD-student's life and Dr. Sishir Gautam, whose serenity in every situation I will never forget. Dr. Marcela van Loo receives a special thanks for always having encouraging words, a smile and a hug. I am grateful to Dr. Georg Lair for his critical thinking and his trust in my abilities. I highly appreciate the dependable laboratory work of Ing. Monika Lex and her care for my computer. I also thank the institute's secretaries DI. Judith Weiss, Mag. Eva Lanz and Eva Motsch, who always extended a helping hand with tedious administrative work and MSc. Lorie and Adam Moreno, who both did a great job in transforming some bulky sentences into nice English writing.

Special appreciation goes to my supervisor Univ.Prof. Dr. Hubert Hasenauer for training me and giving me the opportunity to work in this fascinating field of science, and for his patience with my headstrong ideas.

A full-hearted big thank you goes to Dr. Peter E. Thornton for his incredible support, training and discussions about ecophysiological processes during my five months stay at ORNL in Oak Ridge, Tennessee and at the University of Montana, Missoula, and for the incredible hospitality that he and his wife Michelle showed to me. My appreciation is extended to all of the other staff members, especially to Dr. Gregg Marland, and his wife Bonny. I am grateful to Prof. Steven W. Running for his inspiring broad scientific knowledge and his repeated support and hospitality, also during my second stay with NTSG at the University of Montana.

My research was mainly financed through the projects 'FaKlim', funded by the Cross-border Cooperation Programme Austria-Hungary 2007–2013, 'ARANGE' funded by the EU's 7th Framework Program and 'FarmClim', funded by the Austrian Climate Research Program. The Austrian Marshall Plan Foundation granted me a scholarship for my first stay in the USA.

All my dear friends receive my whole hearted gratitude for their time, thoughts, encouragement and backup even, or especially, when our time together became limited.

My everlasting gratitude goes to my family, to my brothers for their encouragement to get finished and not to forget the fun side of life, to Martin for his love and his support coping with any obstacles that came my way, and above all to my parents for their unending support, love and care.

ABSTRACT

Forest ecosystems are characterised by numerous different, but dependent forest ecosystem functions. The Austrian forest law defines the four main forest functions as: economic, protective, welfare and recreational. In this dissertation I investigated the effects of forest management, stand development and changing environmental drivers on the provision and long-term dynamics of the following forest functions: 1.) Storage of carbon & nitrogen in the soil; 2.) Regulation of the water budget & flood protection; 3.) Productivity; 4.) Welfare & recreation. The forest functions were derived from interrelated ecosystem pools and fluxes of carbon, nitrogen and water, as these correspond with the major ecosystem processes primary production, growth, decomposition, water interception, storage, evapotranspiration and outflow. By means of a paired-stand approach and a study design relying on field data and mechanistic ecosystem modelling using the Biome-BGC model, the effects of forest management, stand development, atmospheric CO₂ concentrations, temperature, precipitation patterns and nitrogen deposition rates were investigated. Forest functions were studied in four different Norway spruce, European beech and American sweetgum dominated forests in different eco-regions in Austria and in Tennessee, USA. Results showed that a plenter forest system compared to an age class system can increase the soil carbon and nitrogen storage and therefore ameliorate degraded soils. Constant or increasing productivity and increasing water use efficiency were projected for the Vienna Woods until 2100, depending on the climate change scenario. Decreasing soil water potentials mainly in low elevations, however, could limit a future productivity increase. Simulations of Norway spruce forests in the Schmittental valley and the analysis of 29 years of river runoff data demonstrated that forest canopy development and ecophysiological control of transpiration change catchment runoff. With a standing timber volume of > 250 m³ outflow was minimised, supporting flood prevention. Consequently, forest management can regulate the provision of a diverse set of forest functions (e.g. flood protection, drinking water supply, net ecosystem carbon storage for climate change mitigation). Foresters can adjust rotation length, stand density and structure, and promote tree species with the desired ecophysiological behaviour, and with these measures influence the flux dynamics in forests.

KURZFASSUNG

Waldökosysteme zeichnen sich durch vielfältige, wenngleich miteinander verbundene Waldfunktionen aus. Das österreichische Forstgesetz kennt vier zentrale Wirkungen des Waldes: die Nutzwirkung, Schutzwirkung, Wohlfahrtswirkung und Erholungswirkung. In dieser Doktorarbeit wurden langfristige Dynamiken 1.) von Kohlenstoff- und Stickstoffspeicherung im Waldboden, 2.) der Regulierung des Wasserhaushalts und der Schutzfunktion gegen Hochwässer, 3.) der Waldproduktivität und 4.) von Wohlfahrts- und Erholungsfunktionen untersucht. Diese Waldfunktionen können vom Kohlenstoff-, Stickstoff- und Wasserhaushalt eines Waldökosystems abgeleitet werden, denn diese beinhalten die zentralen Ökosystemprozesse Primärproduktion, Wachstum, Zersetzung, Niederschlagspeicherung, Verdunstung und Abfluss. Mit Hilfe eines Pärchen-Vergleichs und prozessbasierter Ökosystem-Modellierung mit dem Model Biome-BGC wurden die Auswirkungen von Waldbewirtschaftung, Waldwachstum und sich ändernden Wachstumsbedingungen auf die Waldfunktionen von vier, durch Fichte, Buche oder Amerikanischen Amberbaum dominierten Wäldern in Österreich und im östlichen Tennessee, USA untersucht. Die Ergebnisse zeigen, dass Plenterwälder im Vergleich zu schlagweise genutzten Altersklassenwäldern größere Mengen an Kohlenstoff und Stickstoff im Boden speichern und somit zur Erholung degradierter Böden beitragen. Für den Wienerwald konnte aus einer Simulationsstudie mit vier Varianten von prognostiziertem Klimawandel bis 2100 eine vom Szenario abhängige gleichbleibende oder sogar erhöhte Produktivität abgeleitet werden, wenngleich in den tieferen Lagen die Bodentrockenheit zukünftig einen limitierenden Faktor darstellen könnte. Die Fichtenwälder des Schmittentales zeigten eine deutliche Kontrolle des Abflussgeschehens, wobei bereits bei einem Holzvorrat ab 250 m³ sich der Wasserverbrauch auf hohem Niveau stabilisierte und somit eine entsprechende Schutzwirkung gegeben war. Wasserhaushalts- und Produktivitätsparameter zeigten insgesamt eine starke Abhängigkeit von Bestandes-Entwicklung, Baumart, atmosphärischem CO₂-Gehalt, Temperatur- und Niederschlagsänderungen und Stickstoffdeposition. Mit Hilfe von Waldbewirtschaftung lässt sich somit die Bereitstellung der untersuchten Waldfunktionen (beispielsweise Hochwasserschutz, Trinkwasserbereitstellung und Netto-Kohlenstoffbilanz als Faktor für den Klimaschutz) durch die Umtriebszeit, die Bestandesdichte und die Baumartenwahl steuern.

CONTENT

Preface.....	i
List of peer reviewed publications	ii
Acknowledgements	iii
Abstract	iv
Kurzfassung.....	v
1. Introduction	1
2. Objectives and outline	3
3. Methods.....	5
3.1. Field study following a paired-stand approach.....	5
3.1.1. General	5
3.1.2. Study I	5
3.2. Studies combining field data and mechanistic-modelling	6
3.2.1. General	6
3.2.2. Study II.....	7
3.2.3. Study III.....	7
3.2.4. Study IV	7
4. Data	8
4.1. Study regions.....	8
4.2. Soil data.....	9
4.3. Tree and stand data.....	9
4.4. Runoff data	10
4.5. Daily weather/Climate.....	10
4.6. Atmospheric CO ₂ concentration	11
4.7. Nitrogen deposition	11
5. Analysis and results.....	12
5.1. Storage of C & N in the soil	12
5.2. Regulation of the water budget & flood protection.....	12
5.3. Productivity	13
5.4. Welfare & recreation	14
6. Discussion	15
7. Conclusions	18
References	19
Appendix	23
Appendix I.....	23
Appendix II	31
Appendix III	52
Appendix III-II	68
Appendix IV	69

1. INTRODUCTION

Forests in countries with a long tradition of intensive forest management, such as Austria, have been shaped over the centuries by varying demands for forest products and services, and therefore forest functions. The traditional approach to plan and optimise the historically dominant forest function of timber production required knowledge of general growth characteristics for different tree species and the dependency on site quality. This knowledge was put together in the form of the yield tables, still widely in use today, which tabulate the age and site quality dependent development of stand mean height and diameter at breast height (dbh), stem number, basal area and volume. Yield tables, however, do not cover the diversity of forest functions and potential shifts in growing conditions. A deterioration in site quality manifested as a loss of nutrients stored at a site is the legacy of the historic overexploitation of forests (Glatzel, 1999), whereas the increased atmospheric nitrogen deposition from industry, traffic and agriculture has augmented productivity since the beginning of the Industrial Revolution (Holland et al., 1997). Further, increasing atmospheric CO₂ concentrations, increasing temperatures and shifts in precipitation patterns due to climate change constitute a more recent but significant alteration of the environment in which forests grow (Cramer et al., 2001). In this changing environment, foresters need to manage their forests to optimise timber production but also to secure a large number of different forest ecosystem functions.

The Austrian Forest Act 1975 (amended 2002) defines four principal forest functions, (1) the 'Economic function' (dt. *'Nutzwirkung'*), (2) the 'Protective function' (dt. *'Schutzwirkung'*), (3) the 'Welfare function' (dt. *'Wohlfahrtswirkung'*), and (4) the 'Recreational function' (dt. *'Erholungswirkung'*). These principal forest functions address timber and biomass production (ad 1), the protection of settlements and infrastructure against natural hazards and the conservation of a productive soil (ad 2), the provision of fresh air and clean water as well as balanced climate and water budget (ad 3), and securing forests for regular public recreational activities (ad 4).

The importance and appreciation of the different forest functions change in time and space. People in the mountainous area of Austria (for example in study region II) painfully realised that their overexploited forests could not effectively absorb precipitation, and landslides have repeatedly buried their villages (Hagen, 2003; Pötzelsberger and Hasenauer, 2015a). With the growth and flourishing of large urban areas, the value of forests for welfare and recreation was recognised, leading to preservation incentives, such as in the Vienna Woods, which was protected from complete logging in the second half of the nineteenth century (study region IV). A more recently recognized forest function with global significance is the storage of carbon in the soil and in the biomass to mitigate rising atmospheric CO₂ levels.

People influence how forests fulfil their diverse forest functions via varying forms of forest management. Managing for the provision of these different forest functions requires a detailed knowledge of the functional dependencies between the environment and forest development. In the context of the above-named forest functions, forests can be described as complex open systems that comprise: (A) growing trees with different functional plant compartments (crown, stem, roots), (B) dead biomass, (C) the soil that is the physical footing for the trees, stores water and nutrients and hosts microorganisms for the decomposition of dead organic material, (D) the air that contains CO₂, nutritional N-compounds and water vapour, and (E) the climate system. These components are related and depend on each other via biogeochemical processes, and in addition humans interact via differing management strategies (Figure 1). The vectors for these interactions are fluxes/cycles of carbon, water and nutrients, and solar energy functions as the principle driver. Forest management that ignores these flux dynamics will fail to ensure sustainable forest utilisation and the provision of a diverse set of forest functions in a changing environment. This issue set the stage for my dissertation where I assessed how forest management regulates the provision of key dynamic forest functions based on carbon, nitrogen and water budgets.

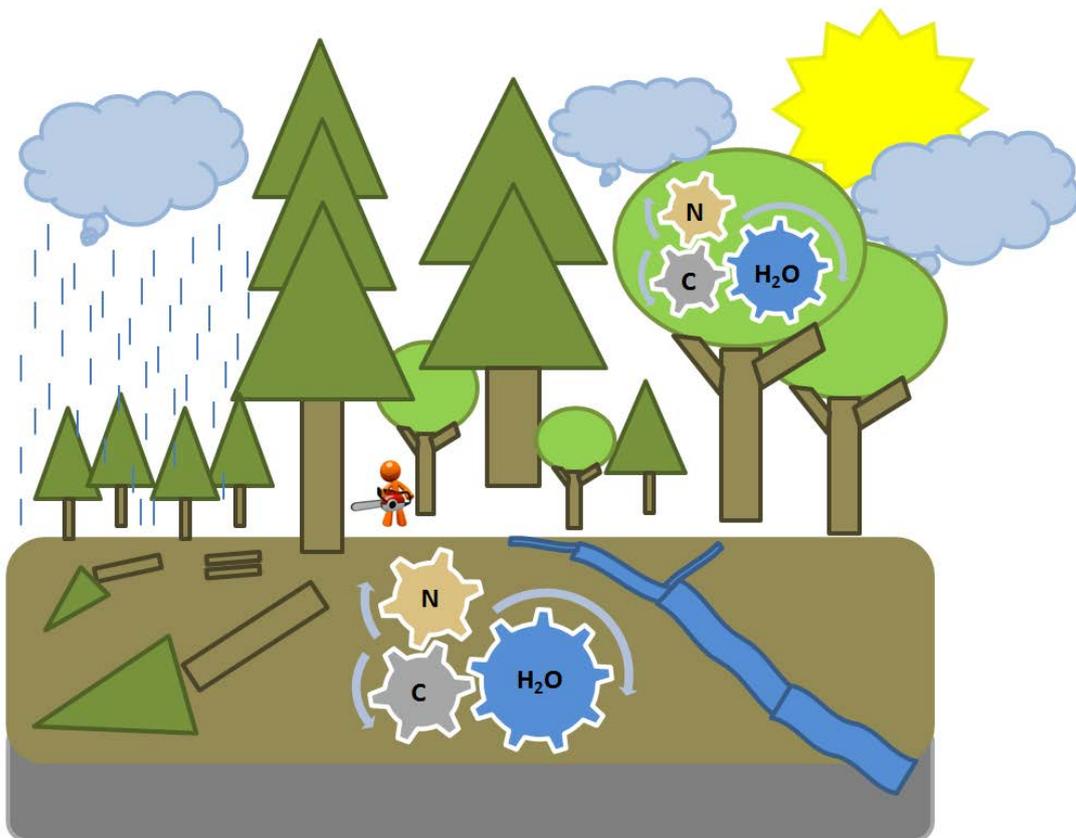


Figure 1 Simple model of a forest with major external and internal drivers (i.e. climate, forest management, stand development) and ecosystem cycles (carbon, nitrogen, water).

2. OBJECTIVES AND OUTLINE

The objective of this dissertation was the assessment of long-term dynamics of forest functions, which are regulated by forest management, and driven by internal changes during stand development and by external drivers including daily weather and long-term changes in the climate system and the composition of the atmosphere. The assessment was done by investigating carbon, nitrogen and water budgets in the forest, that is describing changes in pools and fluxes from which changes in forest functions can be derived. I investigated the long-term dynamics of forest functions for different temperate deciduous and coniferous forests, addressing the following forest functions:

1. Storage of carbon (C) & nitrogen (N) in the soil
2. Regulation of the water budget & flood protection
3. Productivity
4. Welfare & recreation

The above-mentioned forest functions were selected because they cover major aspects of the three ecologically-oriented forest functions defined by the Austrian forest law (Protective, Beneficial and Recreational function, chapter 1). The fourth, remaining forest function, that usually receives the most attention from forest managers, emphasises the economically sustainable production of timber (Economic function), and is referenced indirectly via productivity indicators, first of all net primary production. Important regulators and drivers of long-term dynamics of forest functions are addressed:

- (a) Forest management system
- (b) Stand development
- (c) Weather/Climate
- (d) Atmospheric CO₂ content
- (e) Atmospheric nitrogen deposition rates

Each study in this cumulative dissertation focused on one or more forest functions and investigated dependencies on different combinations of drivers (Figure 2). The approaches to investigate the long-term dynamics of forest functions varied from an individual field study to studies combining field data and mechanistic ecosystem modelling with different degrees of modelling-focus. The scale of the studies ranged from plot (I and III) to catchment (II) and regional (IV). The studied forests were located in different eco-regions in Austria (I, II, IV; chapter 4.1, Figure 3), and in Eastern Tennessee, USA (III; chapter 4.1, Figure 4), where a free-air CO₂ enrichment (FACE) experiment was conducted. Two studies dealt with forests dominated by the coniferous species Norway spruce [*Picea abies* (L.) Karst], two studies focused on the two broadleaved species European beech (*Fagus sylvatica* L.) and American sweetgum (*Liquidambar styraciflua* L.).

- I. Study I was a plot-level field study, that investigated management driven **'Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests'** (Appendix I; Pötzelsberger and Hasenauer, 2015b);
- II. Study II employed field measurements of forest stands and river runoff data as well as mechanistic ecosystem modelling to investigate the **'Forest - water dynamics within a mountainous catchment in Austria'** (Appendix II; Pötzelsberger and Hasenauer, 2015a). The study addressed the influence of Norway spruce stand development and forest management on the forest protection function as it relates to excessive water outflow and therefore floods and landslides in mountainous terrain;
- III. Study III was a plot-level study that investigated the **'Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂'** (Appendix III; Warren et al., 2011b) based on field data from a FACE experiment and mechanistic ecosystem modelling. Forest water budget and productivity indicators were investigated in young experimental American sweetgum stands that developed under ambient and elevated atmospheric CO₂;
- IV. Study IV derived the **'Climate change impacts on key forest functions of the Vienna Woods'** (Appendix IV; Pötzelsberger et al., 2015) from mechanistic ecosystem modelling, focusing on the managed European beech forests in the biosphere reserve Vienna Woods;

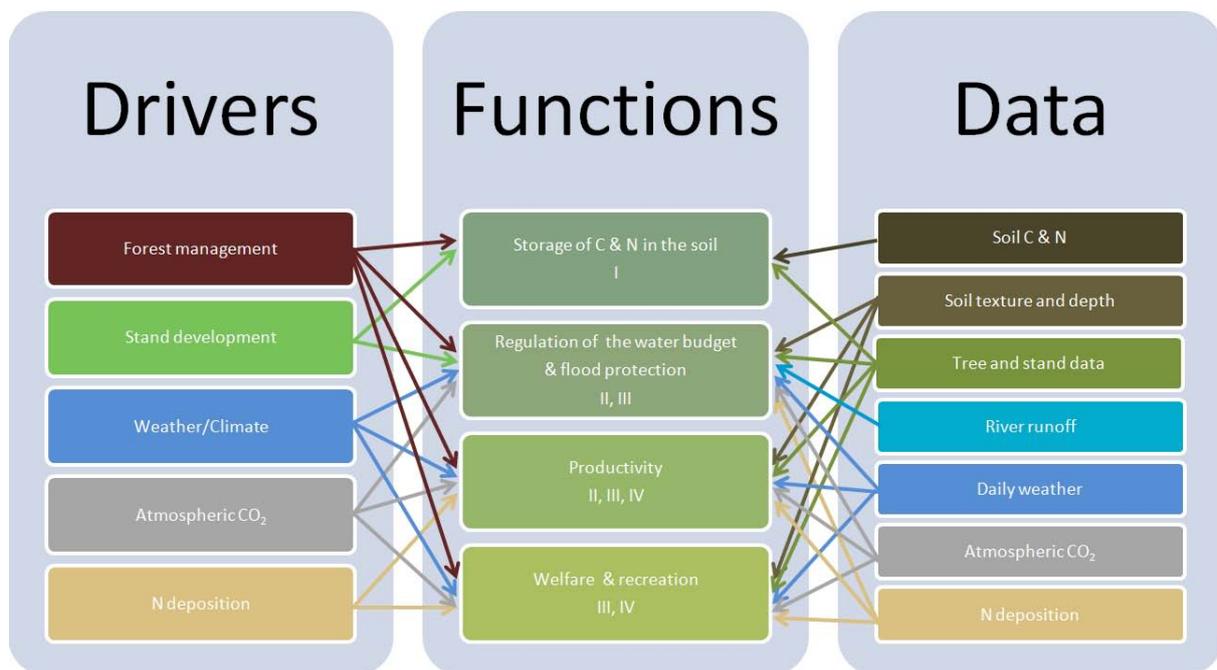


Figure 2 Major interactions investigated between forest ecosystem functions and key ecosystem drivers, and data sets used for the assessment of the different forest functions. Numbers I – IV indicate the study/publication that has special focus on the respective forest function.

3. METHODS

The two principle study designs available to investigate effects of forest management, stand development and changing growing conditions on the provision of forest functions are the experimental-statistical approach and the ecosystem modelling approach. A problem with studying long-term effects on forest functions is that the time frame for obtaining observable responses in the major ecosystem pools and fluxes can easily be as long as several decades (for example due to the length of the characteristic forest development phases or slow decomposition and soil forming processes) and thus are beyond the timeframe of a dissertation. To address this challenge, two approaches for studying long-term responses were chosen:

- Field study following a paired-stand approach
- Study combining field data and mechanistic-modelling with Biome-BGC

3.1. Field study following a paired-stand approach

3.1.1. General

With a paired-stand approach the management effect on different stand characteristics can be determined with statistical methods. The study design requires that the two stands of a pair are in immediate proximity to one another, have essentially identical site conditions and developed from the same original stand until the forest management regime was changed for one of the two paired stands. This paired-stand approach can be seen to replace time by space, relating the approach to the growth series concept (Hasenauer, 1994). The effect of the conversion is determined by conducting measurements within the neighbouring paired stands, instead of comparing measurements from the time when the conversion started with later measurements. An additional advantage of this approach, apart from not having to wait for years, is that all other confounding effects of changes in environmental conditions (for example increasing productivity due to higher nitrogen deposition, impaired productivity due to acid rain, climate change) will have theoretically impacted both stands, thereby isolating forest management as the driving explanatory external variable.

3.1.2. Study I

In study I (Appendix I; Pötzelsberger and Hasenauer, 2015b), the recovery of degraded soils following the conversion of a Norway spruce dominated age class forest (AC) to a single tree selection forest or plenter forest (PL) was studied in the Styrian Koralpe. In the forest enterprise that decided to switch from AC to PL in the early 1960s, 10 pairs of each, AC and PL, on the same site and with common stand history (all AC), were compared. Forest stand data were collected and forest floor and mineral soil carbon and nitrogen stocks and upper soil layer pH were analysed in order to find indicators for a recovery of the soil 50 years after the conversion of the forest management system.

3.2. Studies combining field data and mechanistic-modelling

3.2.1. General

In the presented studies combining field data and mechanistic-modelling, the interactions among forest management, the daily cycling of C, N and H₂O through the ecosystem, gradual changes during stand development and the long-term changes of growing conditions (change over years to centuries) were represented in process-based ecosystem simulations, that were parameterised, driven and validated by different field data sets (see chapter 4). Using the mechanistic ecosystem model Biome-BGC as a diagnostic tool allowed the assessment of changes in forest functions over long time horizons, as the employed ecosystem model simulates changes in pools and fluxes over arbitrary time periods, as long as information on the key model drivers (daily weather, atmospheric CO₂ content, nitrogen deposition) and forest management is available.

The biogeochemical ecosystem model Biome-BGC vs. 4.1 (Thornton et al., 2002) was used with various extensions (Pietsch and Hasenauer, 2006; Pietsch et al., 2005) and corrections issued for version 4.2. This process-based model simulates on a daily time step the cycling of energy, water, carbon and nitrogen within a defined ecosystem and is driven by daily meteorological data. Additional environmental factors employed in the model include atmospheric CO₂ concentration, nitrogen deposition and fixation and physical soil properties (depth, texture). Ecophysiological properties of the simulated ecosystem are defined in an ecophysiological parameter set (epc-file), comprising more than 40 vegetation type/species specific ecophysiological constants (White et al. 2000, Pietsch et al. 2005), whereas common vegetation characteristics are hard coded.

Major ecosystem processes that are calculated are: stomatal conductance (g_s) for CO₂ and water vapour (maximal stomatal conductance g_{sMAX} is reduced depending on the leaf/soil water potential, vapour pressure deficit, solar radiation and night time temperature); assimilation in sunlit and shaded canopy fractions; autotrophic (growth and maintenance) respiration; heterotrophic respiration; gross primary production (GPP); net primary production (NPP); net ecosystem C-storage (NEE); allocation of new carbon and nitrogen; bud break; litter-fall; mineralisation of dead organic material; nitrogen leaching and volatile nitrogen loss; precipitation interception in the canopy; canopy evaporation and transpiration; soil evaporation; soil water storage; and water outflow. Details on the represented processes and on the algorithms can be found in studies II – IV, and in Thornton (1998), White et al. (2000), Thornton et al. (2002), Pietsch and Hasenauer (2006) and Pietsch and Hasenauer (2009).

Biome-BGC is a fully prognostic model where a self-initialisation run (spin-up) is employed to reach an equilibrium state of the ecosystem pools (Pietsch and Hasenauer, 2006). Subsequently, historic land-use simulations account for impacts of forest management on the state of the forest ecosystem, mainly allowing nutrient depletion due to biomass removal and species change. The implemented forest management routines in this model version permit clear cut/planting and thinning interventions.

Clear cut/planting is scheduled by defining the rotation length, the age of the forest for a reference year and the number of rotations before the reference year. With a thinning intervention one can specify relative or absolute amounts of stem and leaf biomass removed from the system, stem biomass transferred to the coarse woody debris pool, leaf and fine root biomass added to the litter pool, coarse root biomass transferred to the coarse woody debris pool, and litter and coarse woody debris removed. All these compartments are characterised by different C/N ratios, such that the extraction of different compartments from the system during harvest and thinning has different effects on the productivity of the site. The species or vegetation type can be selected at each planting. Different tree species influence the ecosystem cycles due to their differing ecophysiological behaviour, growth patterns (allocation of assimilates to the various plant compartments) and C/N ratios of the various ecosystem compartments (Pietsch et al., 2005).

3.2.2. Study II

In study II (Appendix II; Pötzelsberger and Hasenauer, 2015a), Norway spruce development, plot outflow and catchment runoff were simulated on a 100 m by 100 m grid in the 7.3 km² intensively managed mountainous study-catchment in the Schmittental valley, Salzburg. We analysed interactions of forest growth and the water budget, driven by forest management, stand development, site conditions and daily weather data, and assessed the forest protection function against excessive water outflow that occasionally triggers floods and landslides. We used Biome-BGC and stand and site information from 21 Norway spruce stands and 29 years of river runoff data for model validation.

3.2.3. Study III

In study III (Appendix III; Warren et al., 2011b), conducted at a FACE experiment in an American sweetgum plantation in Oak Ridge, Tennessee, we parameterised Biome-BGC for American sweetgum growing under elevated atmospheric CO₂ concentrations (eCO₂, target CO₂ concentration 525ppm – 555ppm) and ambient CO₂ concentrations (aCO₂) and performed mechanistic ecosystem simulations which covered the first eleven years (1998 – 2008) of the 12-year experiment. Specifically, we investigated the impact of eCO₂ on the forest water budget and productivity indicators.

3.2.4. Study IV

In study IV (Appendix IV; Pötzelsberger et al., 2015), ecophysiological, water budget and productivity indicators were simulated for the beech forests of the Vienna Woods. We further derived indications of changes in forest functions relevant to welfare and recreation. We collected field data of beech forests in and around the study area for model validation. Then we conducted climate change simulations with Biome-BGC for European beech on a 1 km by 1 km grid in the 1400 km² study area using (i) regional climate change scenarios based on the IPCC (2000) greenhouse gas emission scenarios A1B and B1 and (ii) a self-defined precipitation scenario for the horizon 2100.

4. DATA

4.1. Study regions

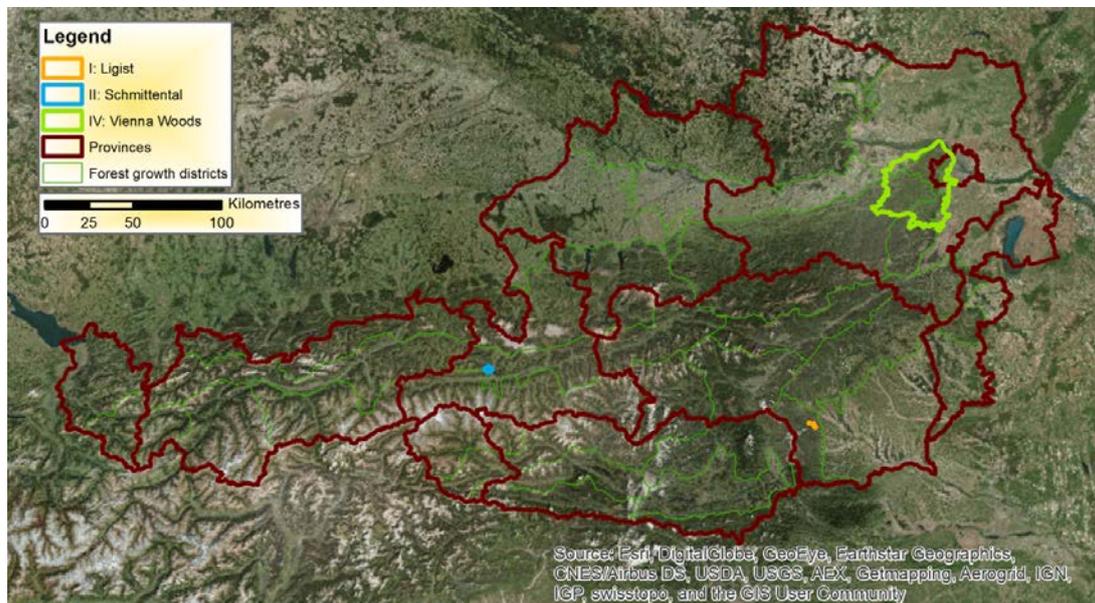


Figure 3 Satellite image of Austria with the forest growth districts after Kilian et al. (1994) and the three study regions Ligist (study I), Schmittental (study II) and Vienna Woods (study IV).

The Austrian studies I, II, IV (Figure 3) are located within the different eco-regions or forest growth districts '5.4 West-Styrian Mountains' (study I), '2.2 Northern Transitional Alps – Eastern Part' (study II), '4.2 Northern Limestone Alps – Eastern Part' and '5.1 Lower Austria – Eastern edge of the Alps' (study IV; Kilian et al., 1994). Study III was conducted in East Tennessee, USA (Figure 4).

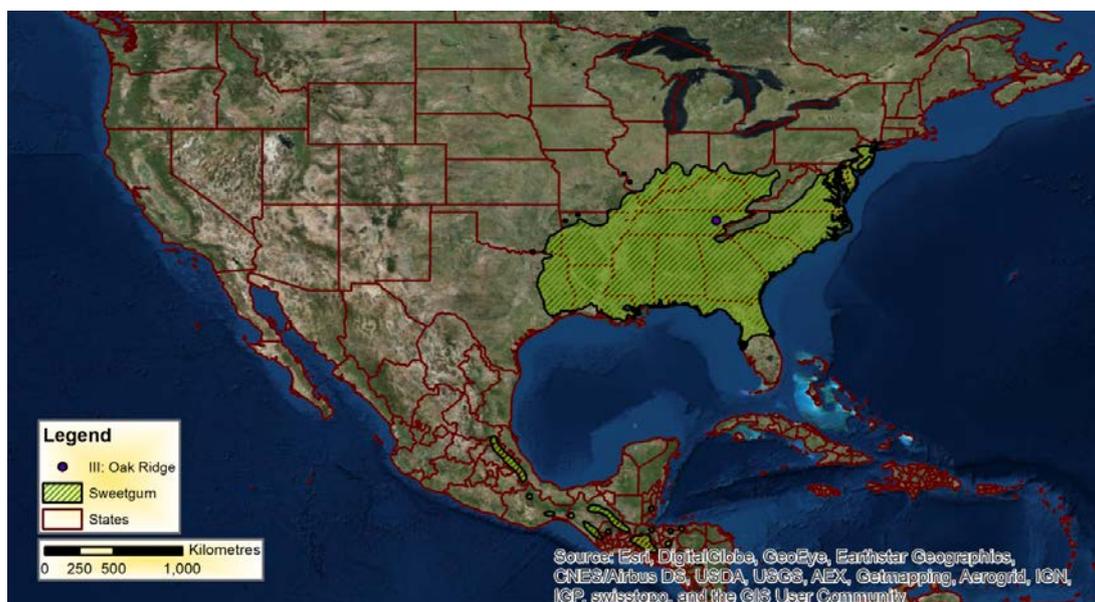


Figure 4 The natural distribution of American sweetgum, *Liquidambar styraciflua* L. (green hatched) with dispersed subpopulations (black dots), after Little (1971), and location of the study site in Oak Ridge, Tennessee, USA.

4.2. Soil data

Soil carbon and nitrogen stocks were analysed in study I. One 15 m x 15 m sampling plot was selected in a representative area of every forest stand, avoiding skidding trails and large canopy openings. Forest floor and mineral soil samples were taken at every corner of a sampling plot. If obstacles were present, such as trunks, stems, big roots or rocks, the sampling location was shifted according to a predefined scheme. Living understory vegetation was removed. Forest floor was collected completely using a 550 cm² frame. The mineral soil was sampled at 0 – 20 cm, 20 – 50 cm and > 50 cm depth. Dry soil density, carbon and nitrogen concentration and pH were determined in the laboratory.

As input to Biome-BGC, soil depth and texture were needed for studies II-IV. For the Austrian studies, soil depth and sand, silt and clay content were interpolated from the Austrian National Forest Soil Survey data (Englisch et al., 1992) as described by Petritsch and Hasenauer (2007). For the Oak Ridge FACE study, soil depth and texture were available from the experiment (Warren et al., 2011b).

4.3. Tree and stand data

In study I, forest stand data (dbh, height, volume, tree number) were obtained by angle-count sampling (4 samples per stand) according to Bitterlich (1948). In studies II and IV, conducted in the Schmittental valley and the Vienna Woods, forest stand and site information was needed for model validation. The validation data were required to cover those forest stand and site situations that the model later was applied to. We obtained stand volume and stand age from angle-count sampling for 21 Norway spruce stands (study II; Pötzelsberger and Hasenauer, 2015a) and from 25 European beech permanent observation plots (study IV; Pötzelsberger et al., 2015). The permanent observation plot data were obtained from the Department of Forest and Soil Sciences, BOKU demonstration forest, located in the mountain range Rosalia, Lower Austria (11 plots), the forests of the Heiligenkreuz monastery in the municipality Wienerwald (6 plots), a forest in the municipality Windischhütte also within the Vienna Woods (1 plot) and from ICP Forests Level I plots (7 plots). Plot size ranged from 225 m² to 1 ha, stand age varied from 25 to 170 years, the number of re-measurements ranged from one to three and the re-measurement interval was 5 or 6 years.

In study III, at the Oak Ridge FACE experiment, detailed morphological and physiological data were available from the experiment. The data that could be utilised for the parameterisation of Biome-BGC for the study species American sweetgum covered all-season LAI curves; C/N ratios of leaves, fine roots, litter and wood; increment data of leaves, fine roots, coarse roots and stem to determine the various required allocation ratios; specific leaf area (SLA) of sun and shade leaves; maximal stomatal conductance; response data of stomatal conductance vs. VPD (Appendix III-II). The CO₂-treatment required two sets of ecophysiological parameters, one for ambient CO₂ and one for elevated CO₂.

4.4. Runoff data

River runoff data with a high temporal resolution are very valuable for the validation of catchment runoff simulation, and there are only few small hydrological catchments (< 25 km²) in the Alps with long-term, high-resolution data on precipitation and runoff (Geitner et al., 2009). The Schmittental valley in Salzburg, Austria is one of them. For study III, daily river runoff data from the Schmittenbach river, which drains the mountainous 10 km² Schmittental catchment were obtained for the period 1981 – 2009. The gauged catchment has a size of 7.3 km² and an elevation range from 905 m to 1965 m. Runoff data unsuitable for further analysis were caused by measurement device breakdowns, ice, debris or mud. A total of 874 days was missing or flawed as a result. Erroneous data were dismissed and no gap-filling was done, but the respective days were later also excluded from catchment runoff simulation results to allow an unbiased comparison with the observations.

4.5. Daily weather/Climate

The Biome-BGC modelling studies required daily weather data, including minimum and maximum temperature (Tmin, Tmax), precipitation (Prcp), solar radiation (Srad) and vapour pressure deficit (VPD). Location specific data are necessary for the analysis of processes with a high temporal resolution (days, weeks). For Austria (studies II and IV) data from 1960 up to present were derived from more than 400 Austrian-wide climate stations, provided by the Austrian Central Institute for Meteorology and Geodynamics (ZAMG), and stations in the neighbouring countries to avoid edge effects at the border. Temperature (Tmin, Tmax) and Prcp were interpolated and Srad, VPD and length of day were calculated by DAYMET (Thornton et al., 1997). DAYMET is a climate interpolation and simulation tool validated for Austria (Hasenauer et al., 2003; Petritsch, 2002; Thornton et al., 2000). To address terrain related variations in the interpolation procedure a detailed digital elevation map was used to calculate slope, aspect and angles to the horizon in the east and in the west. At the Oak Ridge FACE site (study III), daily weather data were calculated from hourly observations at the experimental site for the years 1998 to 2008. In Biome-BGC simulations, the available climate data commonly are repeatedly and (in the non-observation years) randomly used for the whole simulation period, which usually covers a few thousand years, including the model spin-up.

Study IV demanded the acquisition of regional climate change scenarios for the Vienna Woods area. The two widely used global greenhouse gas emission scenarios A1B and B1 (IPCC, 2000) were selected and the corresponding climate simulation data CLM_A1B_1_D3 and CLM_B1_1_D3 (Lautenschlager et al., 2009a, 2009b) obtained for the years 2010 – 2100. From these data and a self-defined precipitation scenario (at maximum 30% higher winter and lower summer precipitation), four different climate change scenarios for the period 2010 to 2100 were derived, 1.) A1B and no change in precipitation (A1B), 2.) A1B and precipitation changes as outlined above (A1B + Prcp), 3.) B1 and no change in precipitation (B1) and 4.) B1 and precipitation changes as outlined above (B1 + Prcp).

4.6. Atmospheric CO₂ concentration

The partial pressure of CO₂ in the atmosphere together with the stomatal conductance determine the amount of CO₂ available for photosynthetic carbon assimilation. In standard Biome-BGC simulations the IPCC global annual mean atmospheric CO₂ concentration data set IS92a (Enting et al., 1994; IPCC, 1992) is used. For simulation years before the start year of the data set (year 1765) the CO₂ concentration is kept at the preindustrial level given by the first entry in the data set.

For the Oak Ridge FACE site, the historic development was treated the same, but local CO₂ concentration values were used from data available since the project start. The half-hourly values of the ambient and the elevated CO₂ experiments, recorded during the growing season, were averaged to annual means as suitable for the simulations. Annual means in the eCO₂ plots ranged from 527ppm to 558ppm and from 381ppm to 401ppm in the aCO₂ plots.

4.7. Nitrogen deposition

Current nitrogen deposition rates for Austria (for study II and IV) were derived from a 1 km x 1 km N-deposition map (Eastaugh et al., 2011). That map is based on two studies on wet nitrogen deposition (Schneider, 1998) and dry nitrogen deposition (Placer and Schneider, 2001) conducted by the Environment Agency Austria (Umweltbundesamt, UBA), Vienna. The deposition map can be considered representative for the last 20 years since deposition rates of NO_x and NH₃ have been reported to be near stable since the early 1990s (Anderl et al., 2014). For study III at the Oak Ridge FACE site, the current N-deposition had been measured to be 12 kg N ha⁻¹ y⁻¹ (Johnson et al., 2004).

Preindustrial N-deposition in temperate forests was estimated having amounted to 1 kg N ha⁻¹ y⁻¹ by Holland et al. (1999). In between this preindustrial level and the current N-deposition levels of studies II-IV the N-deposition trends were assumed to be analogue to the atmospheric CO₂ trend derived from the IS92a data set (Enting et al., 1994; IPCC, 1992).

5. ANALYSIS AND RESULTS

Key relations between forest functions and ecosystem drivers were investigated in four separate studies, given the various different forest functions that are defined by the Austrian law and that are of fundamental importance to the Austrian people, either living on the countryside in often mountainous terrain, or in urban areas (chapter 1), and given the numerous interdependencies between forest functions and ecosystem drivers (chapter 2, Figure 2). The studies mostly (studies II-IV) covered more than one forest function because of the natural interrelations of the forest functions and the close link to the underlying C, N and H₂O cycles. The studies also dealt with changes of two or more ecosystem drivers at the same time, since in long-term studies/experiments the change in a studied environmental driver appears together with forest growth, defined as an internal driver. As people manage forests with the goal to optimise their target forest functions, I decided to present the results arranged by forest functions.

5.1. Storage of C & N in the soil

The choice of the forest management system had an impact on the soil carbon and nitrogen stores (Appendix I; Pötzelsberger and Hasenauer, 2015b). Plenter forests on average had a 9 Mg C ha⁻¹ or 11% higher mineral soil carbon storage and a 0.4 Mg N ha⁻¹ or 11% higher mineral soil nitrogen storage in 0 – 20 cm depth. Considering also the litter layer and the full depth of the sampled mineral soil (> 50 cm), average soil carbon storage in the plenter forests was 170 Mg C ha⁻¹ whereas age class forests stored 158 Mg C ha⁻¹. This difference was not significant though. In contrast, total nitrogen storage in the soil was significantly higher, with 6.8 Mg N ha⁻¹ in PL and 6.1 Mg C ha⁻¹ in AC.

5.2. Regulation of the water budget & flood protection

In the simulated mountainous Norway spruce stands transpiration (Tr) and evaporation (Ev) increased with the leaf area index (LAI) during stand development (Appendix II; Pötzelsberger and Hasenauer, 2015a). The increase in Tr levelled off, whereas the increase in Ev became more pronounced with higher LAI. Soil Ev decreased but Ev of intercepted water in the canopy increased markedly. Canopy Tr in the American sweetgum FACE site had been measured during four years, and was simulated for the whole treatment period, defining a reduction of maximal stomatal conductance of 10% under the treatment specific eCO₂ levels of 525ppm – 555ppm (Appendix III; Warren et al., 2011b). In non-drought years, measured annual reduction in Tr due to eCO₂ ranged from 10% to 16%, and simulated Tr reduction ranged from 11% to 16%. In the Vienna Woods simulations, where no reduction in g_{SMAX} with increasing CO₂ had been defined for beech, stand Tr and Ev under the four climate change scenarios showed differentiated trends (Appendix IV; Pötzelsberger et al., 2015). Ev increased under A1B whereas Tr decreased under A1B + Prcp and B1 + Prcp and so did evapotranspiration (ET).

Water use efficiency (WUE) is an ecophysiological characteristic that integrates water consumption and productivity, and can be expressed in various ways (Pallardy, 2008). Simulated WUE (NPP/ET) for the mountainous Norway spruce forests was lowest for young stands with $LAI < 1$, highest for stands with a LAI between 2 and 3, and stabilised at an about 20% lower level for older, denser stands (about $0.65 \text{ g C m}^{-2} \text{ mm}^{-1} \text{ H}_2\text{O}$). For American sweetgum at the Oak Ridge FACE site simulated WUE defined as NPP/ET, averaged over the treatment period 1998 – 2008, increased by 15% (from $1.04 \text{ g C m}^{-2} \text{ mm}^{-1} \text{ H}_2\text{O}$ to $1.2 \text{ g C m}^{-2} \text{ mm}^{-1} \text{ H}_2\text{O}$, data not shown). The annual average WUE increase ranged from 11% to 20%. Simulated WUE defined as NPP/Tr increased on average by 19% (from $1.31 \text{ g C m}^{-2} \text{ mm}^{-1} \text{ H}_2\text{O}$ to $1.56 \text{ g C m}^{-2} \text{ mm}^{-1} \text{ H}_2\text{O}$). For European beech in the Vienna Woods an increase of WUE (NPP/Tr) during the climate observation period (1960 – 2009) and under all four climate change scenarios (2010 - 2100) was suggested, with the highest increase for A1B + Prcp, the scenario with the higher temperature increase plus exacerbated water supply (compared to B1; chapter 4.5). The relative increase between the mean for the period 1960 – 1979 and the mean for the period 2081 – 2100 under A1B + Prcp was 25%. Despite the increase in WUE the beech forest summer soil water potentials mostly decreased under climate change, with lowest levels reached in low elevations.

Water not consumed by the forest and not held by the soil leaves the forest as outflow. Annual outflow in the mountainous Norway spruce forests showed a strong negative relationship with LAI (Appendix II; Pötzelsberger and Hasenauer, 2015a). For young homogenous stands outflow declined until a standing volume of about 250 m^3 was reached, and stabilised thereafter. For catchment runoff estimates derived from plot outflow simulations a hydraulic transfer function was applied to account for the retention of plot outflow in the catchment until discharged into the river. The comparison of river runoff measurements with estimated weekly catchment runoff showed consistent patterns, with some uncertainty of runoff estimates during peak snowmelt in spring and extreme rainfall events in summer. Under $e\text{CO}_2$ at the sweetgum FACE site, annual water outflow was simulated to increase by 15% on average (Appendix III; Warren et al., 2011b), ranging from +6% to +40%. Outflow from beech forest in the Vienna Woods was projected to increase under A1B + Prcp and B1 + Prcp, caused by an increase in winter outflow (Appendix IV; Pötzelsberger et al., 2015).

5.3. Productivity

For the mountainous Norway spruce forests a strong positive correlation between the two productivity indicators LAI and timber volume was simulated, given a timber volume $< 250 \text{ m}^3$ (Appendix II; Pötzelsberger and Hasenauer, 2015a). This correlation disappeared with higher timber volume. Simulated LAI was negatively correlated with elevation in mid to high elevations (1,250 – 1,850 m) and positively correlated with measured stand density index (SDI; Reineke, 1933). Over the course of the sweetgum FACE experiment simulated annual maximum LAI under $a\text{CO}_2$ and $e\text{CO}_2$ varied around 4.5 and 4, respectively, and thus was up to 20% and 45% lower than measured LAI, whereas in most of the years higher LAI under $e\text{CO}_2$ was measured (Appendix III; Warren et al., 2011a, 2011b).

Measured NPP (Norby et al., 2010) as well as simulated NPP increased due to eCO₂, however the simulated increase was less pronounced. For beech forests under climate change a significant increase in LAI (+9% – +21%) and GPP (+15% – +30%) was projected in all scenarios but one (B1 + Prcp), whereas NPP increased only under one scenario (A1B; Appendix IV; Pötzelsberger et al., 2015). Autotrophic respiration increased under all four scenarios. Net primary production was highest in regions with high N-deposition (close to the city) and showed a positive trend with elevation. Net ecosystem carbon storage NEE was positive under all scenarios and increased under A1B.

Investigated dependencies between the major elements of the C, N and H₂O budgets as discussed above and key factors causing changes in forest functions, including forest management, stand development, elevated atmospheric CO₂, climate change and N-deposition are summarised in Table 1.

Table 1 Synthesis of the analysed dependencies between major elements of carbon, nitrogen and water cycles and the key factors causing changes in forest functions as considered in studies I-IV, including changes in the forest management system; during stand development; with elevated atmospheric CO₂; temperature increase; temperature increase combined with shifts in precipitation patterns (lower summer, higher winter precipitation); and increased nitrogen deposition. '+' indicates an increase, '-' a decrease and '~' no change; '/' indicates that the relationship has not been investigated; factor 'eCO₂' refers to study III considering a reduction in g_SMAX for American sweetgum due to elevated CO₂, (+eCO₂) refers to study IV assuming no reduction in g_SMAX for European beech due to elevated CO₂.

	Management	Stand development	eCO ₂	T (+eCO ₂)	T + Prcp (+eCO ₂)	N-deposition	
Soil	C&N	+	/	/	/	/	
	Tr	+ - ~	+ ~	-	~	-	/
Water budget	Ev	+ - ~	+ ~	+ - ~	+ ~	~	/
	WUE	+ - ~	+ - ~	+	+	+	/
	Of	+ - ~	- ~	+	~	+	/
Productivity	LAI	- ~	+ ~	+ - ~	+	+ ~	/
	NPP	- ~	/	+ ~	+ ~	~	+
	NEE	/	/	/	+ ~	~	/
	AR	/	/	/	+	+	/

Tr...Transpiration; Ev...Evaporation; WUE...Water use efficiency; Of...Outflow; LAI...Leaf area index; NPP...Net primary production; NEE...Net ecosystem exchange; AR...Autotrophic respiration.

5.4. Welfare & recreation

Forest functions relevant to welfare and recreation were derived from the major ecosystem cycles of carbon, nitrogen and water. Such, changes in the provision of these forest functions were investigated based on the presented studies dealing with the regulation of the forest water budget and forest productivity. Productivity indicating the stability of forests, LAI as measure of forest crown development, NEE describing the net carbon storage of the forest ecosystem, evapotranspiration influencing latent heat fluxes and water outflow and thus drinking water supply all have impacts on welfare and recreation.

6. DISCUSSION

Forest functions are manifold and are summarised by the Austrian forest law as economic, protective, welfare and recreational function. The forest branch of the Institute for Environment and Sustainability, joint research centre of the European Commission (JRC - Forest Action, 2014) recognises that 'forest ecosystem functions support the provision of ecosystem services to humans' and provides a comprehensive list of goods and services provided by forests, comprising wood and non-wood products (e.g. biomass based energy); climate regulation (e.g. C-sequestration); pollution control; soil protection and formation (e.g. erosion control); nutrient cycling; biodiversity protection; water regulation and supply; recreation; and disturbance regulation. The cycling of C, N and H₂O through the forest ecosystem lies at the core of a majority of these forest ecosystem goods and services and relates these goods and services among each other. This makes mechanistic ecosystem modelling an appropriate diagnostic tool for assessing impacts of changes in the drivers of these ecosystem cycles/processes.

Forest management plays an especially fundamental role in the future provision of ecosystem goods and services as it heavily influences the ecosystem flux dynamics by changing forest structure and density, rotation length and species composition. The comprehension of the functional dependencies among forest ecosystem processes, site conditions and forest management measures (Table 1) is a prerequisite for sustainable forest management and the optimisation of the target forest functions, especially under changing growing conditions. Therefore, in this thesis those forest functions that can be derived from the cycling of C, N and H₂O were investigated, including the storage of C & N in the soil, the regulation of the water budget & flood protection, forest productivity, welfare & recreation, using a paired-stand approach and studies combining field data and mechanistic-modelling.

It could be shown that the shift of the forest management system from age class forest to plenter forest had a positive impact on soil C and N stores (Appendix I; Pötzelsberger and Hasenauer, 2015b). This gives forest managers the ability to ameliorate soils degraded by historic land use. Enhancing carbon and nitrogen in the forest soil is a means to improve site productivity (storage of nutrients, filter capacity of the soil). The additional storage of carbon in the forest soil of 9 Mg C ha⁻¹ in the upper 20 cm of the soil amounts to almost 9% of the average amount of carbon stored in Austrian forest soils [106 Mg C ha⁻¹, (Weiss et al., 2000)] and thus is a relevant contribution to climate change mitigation. Forests also modify the site water balance, for example during stand development and as a reaction to changing environmental conditions. Study II (Appendix II; Pötzelsberger and Hasenauer, 2015a) showed that with increasing LAI in the early phase of stand development Tr and Ev (Ev mostly from intercepted precipitation) increased and Of decreased. In the studied Norway spruce system, which is the most widespread forest type in Austrian mountainous areas, a strong reduction in outflow was already reached at a timber volume of about 250 m³, supporting flood prevention. Catchment runoff analysis confirmed the important role of forests in the regulation of the catchment water balance.

The definition of the rotation length therefore is a forest management measure that changes the temporal share of the early development stage with low water consumption and the later stage with fully developed crown coverage. Forest managers also may promote tree species with the preferred ecological behaviour (Pietsch et al., 2005), showing either high water consumption in areas where flood protection is crucial (low WUE, high productivity), or having lower water consumption (high WUE) in regions where severe water limitations under climate change are expected.

The regulatory effect of forests on the water budget, however, is subject to changes under increasing atmospheric CO₂ concentration and climate change. Understanding possible responses to such changes is important for forest managers to ensure the future provision of forest functions. Increases in WUE (an important indicator relevant for drinking water supply, flood protection and a plant's ability to assimilate carbon under water limiting conditions) were diagnosed for American sweetgum under eCO₂ (Appendix III; Warren et al., 2011b) and for European beech under climate change (Appendix IV; Pötzelberger et al., 2015). Further, stomatal conductance is a central element in the regulation of the water budget and productivity. The response of g_s to eCO₂ and the underlying mechanisms are not yet fully understood (Medlyn et al., 2011) and the effect varies among plant functional types and among woody species (Ainsworth and Rogers, 2007; Norby et al., 1999; Saxe et al., 1998). For sweetgum a reduction in g_{sMAX} was assumed in accordance with measurements, whereas for beech it was not (in different studies published by various authors g_s reductions ranged from > 30% to no significant reduction, see Appendix IV; Pötzelberger et al., 2015).

If eCO₂ decreases g_s for a species, this immediately leads to a reduction in transpiration and thus water consumption. If the CO₂ fertilisation effect at the same time increases productivity and leads to an increase in LAI, the initial water savings may be counterbalanced. In young forest stands, for example, increased productivity due to elevated CO₂ can cause faster canopy development (Norby et al., 1999). The faster increase of LAI in turn will increase the water consumption at a site and consequently reduce site water outflow. This decreases on the one hand the water yield for drinking water but on the other hand improves the protection function against excessive runoff. However, LAI can also be reduced under extreme events. In the extreme drought year of 2007 measured later-summer Tr was reduced by up to 45% under eCO₂ (Warren et al., 2011a), connected to leaf loss. Leaf loss possibly was caused by the negative effect of conductance reduction on latent heat loss and on the leaf carbon balance. Leaf damage due to heat/drought and premature leaf loss are not yet integrated in Biome-BGC. An integration of such a mechanism would improve the representation of the drought impact on the site water balance (although the average simulated reduction of annual Tr under eCO₂ agreed well with measurements). It could also improve the reliability of productivity estimates, extending to a reduction of productivity in the year following the drought due to a depleted carbon storage. Eventually, this would allow a better assessment of alternative forest management options under climate change.

It is predicted that forest managers will have to respond to drought effects in the future and therefore will need to show more attention to stand structure, harvesting regimes and water management (Hlásny et al., 2014; Lindner et al., 2010; Seidl et al., 2011). For beech Chakraborty et al. (2013) observed drought damage impacting the regeneration in the understory of adult trees. An adaptation of the shelterwood system could alleviate the situation for the understory if the coverage of the overstory and thus its water consumption is reduced in time. In the beech forests of the Vienna Woods productivity levels under climate change stayed at current levels or even increased. However, correlated with low soil water potentials in low elevations, the NPP increase was limited (Appendix IV; Pötzelsberger et al., 2015). An effect of a possibly water-limited situation on the understory, however, could not be tested since Biome-BGC does not include different tree layers.

A further, debated phenomenon in climate change impact studies is the downregulation of productivity due to nitrogen or generally nutrient limitation under CO₂ enrichment. This phenomenon has been observed in several CO₂-fertilisation experiments (Luo et al. 2004), including the sweetgum FACE site, where initially stimulated productivity decreased after a couple of years (Oren et al. 2001; Iversen and Norby 2008). Biome-BGC simulations for the FACE study also indicated an increasing limitation of growth by lack of nitrogen. An increasing difference between theoretically possible assimilation (considering LAI, g_s, CO₂, T) and assimilation actually permitted by the N-supply, providing the N required for the allocation of assimilated C to the different plant tissues with fixed C/N ratios, was observed (data not shown). The N-limitation triggered increasing fine-root production especially under eCO₂ (Norby et al., 2010), almost doubling the epc-allocation parameter of 'new fine-root C relative to new leaf C' under eCO₂. This parameter probably caused the pronounced underestimation of simulated LAI under eCO₂. In Austria, however, 94.4% of the forests exceed the critical loads for eutrophication causing N-deposition (Obersteiner and Offenthaler, 2008), including the Vienna Woods. Therefore, potentially increasing future forest productivity is unlikely to be N-limited in most parts of Austria.

Forest managers need to be aware of how changes in the forest productivity and the water budget impact the provision of ecosystem services related to welfare and recreation. Positive NEE, projected for the Vienna Woods under climate change, under the assumption that felled timber is transported out of the forest (and stored), constitutes a mitigation effect on climate change and thus can be seen as a positive effect on welfare. Reduced Tr under eCO₂ and climate change decreases the evaporative cooling in the forest canopy and therefore increases the temperature locally. However, higher LAI improves shading under the forest canopy for visitors seeking relaxation in the forest. With changes in water outflow the water yield from the forest that potentially can be used as drinking water resource is impacted. Water savings due to a stomatal response to eCO₂ can increase the water yield, if this effect is not counterbalanced by significantly increasing LAI and thus interception and transpiration. Eventually, forest management that ensures forest productivity is a general but important requirement for a sustainable drinking water supply (Richards et al., 2012) because forests ensure a balanced water cycle and the filtering of pollutants (Blume et al., 2010; Dudley and Stolton, 2003).

7. CONCLUSIONS

Internal and external drivers govern the long-term dynamics of forest ecosystem functions. Forest functions are connected among each other via feedback loops between pools and fluxes of carbon, nitrogen and water in the forest ecosystem. Forest management is a tool to optimise the provision of different forest functions given changing forest properties with stand development and changing growing conditions due to expected climate change. It could be shown that the shift from age class forests to single tree selection forests ameliorated degraded soils by increasing soil C and N storage. Forest management can also improve either flood protection or drinking water supply by adjusting rotation length, stand density and species composition, considering species specific growth, crown development, maximal stomatal conductance, transpiration regulation and water use efficiency.

Forest productivity is the basis for all analysed forest functions because of its central position in the energy, C, N and H₂O cycles. Projections of productivity indicators (LAI, NPP, NEE) and the water budget under climate change based on mechanistic-modelling allowed conclusions on requirements for future forest management. The beech forests of the Vienna Woods, for example, were projected to increase their WUE and primary production or keep current productivity levels, depending on the climate change scenario, even though low soil water potentials in low elevations were projected to limit the productivity increase. Consequently, no significant change in forest management requirements could be derived for the Vienna Woods. Still, forest management may be required to be especially attentive concerning stand structure/density as it influences the water budget. Regardless of the forest function desired, forest managers need to be aware that any forest operation influences the flux dynamics within forest ecosystems and that careful forest management planning becomes imperative under changing growing conditions, most importantly climate change.

REFERENCES

- Ainsworth, E.A., Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant, Cell Environ. Environ.* 30, 258–70.
- Anderl, M., Jobstmann, H., Köther, T., Lampert, C., Moosmann, L., Pazdernik, K., Pinterits, M., Poupa, S., Stranner, G., Zechmeister, A., 2014. Austria's Annual Air Emission Inventory 1990 – 2012. Environment Agency Austria, Vienna. pp. 37.
- Bitterlich, W., 1948. Die Winkelzählprobe (The angle-count sample). *Allg. Forst- und Holzwirtschaftszeitung.* 59, 4–5.
- Blume, H.-P., Brümmer, G.W., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., Wilke, B.-M., 2010. Scheffer/Schachtschabel Lehrbuch der Bodenkunde (Textbook of Soil Science), 16th ed. Spektrum Akademischer Verlag, Heidelberg. pp. 569.
- Chakraborty, T., Saha, S., Reif, A., 2013. Decrease in Available Soil Water Storage Capacity Reduces Vitality of Young Understorey European Beeches (*Fagus sylvatica* L.)—A Case Study from the Black Forest, Germany. *Plants.* 2, 676–698.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R. a., Brovkin, V., Cox, P.M., Fisher, V., Foley, J. a., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., Young-Molling, C., 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models. *Glob. Chang. Biol.* 7, 357–373.
- Dudley, N., Stolton, S., 2003. Running Pure: The importance of forest protected areas to drinking water. The World Bank/WWF International, Washington D.C., USA; Gland, Switzerland. pp. 112.
- Eastaugh, C.S., Pötzelsberger, E., Hasenauer, H., 2011. Assessing the impacts of climate change and nitrogen deposition on Norway spruce (*Picea abies* L. Karst) growth in Austria with BIOME-BGC. *Tree Physiol.* 31, 262–74.
- Englisch, M., Karrer, G., Mutsch, F., 1992. Österreichische Waldboden Zustandsinventur (Austrian National Forest Soil Survey). *Mitteilungen der Forstl. Bundesversuchsanstalt, Wien.* 168, pp. 247.
- Enting, I.G., Wigley, T.M.L., Heimann, M., Scientific, C., 1994. Future emissions and concentrations of carbon dioxide: Key ocean/atmosphere/land analyses. Division of Atmospheric Research Technical Paper no. 31. CSIRO, Australia. pp. 127.
- Geitner, C., Mergili, M., Lammel, J., Moran, A., Oberparleiter, C., Meißl, G., Stötter, H., 2009. Modelling peak runoff in small Alpine catchments based on area properties and system status, in: Veulliet, E., Johann, S., Weck-Hannemann, H. (Eds.), *Sustainable Natural Hazard Management in Alpine Environments.* Springer Berlin Heidelberg, Berlin, Heidelberg. pp. 103–134.
- Glatzel, G., 1999. Historic forest use and its possible implication to recently accelerated tree growth in Central Europe, in: Karjalainen, T., Spieker, H., Laroussine, O. (Eds.), *Causes and Consequences of Accelerated Tree Growth in Europe.* EFI Proceedings No 27. pp. 65–74.
- Hagen, K., 2003. Wildbacheinzugsgebiet Schmittbach (Salzburg) - Analyse des Niederschlags- und Abflussgeschehens 1977-1998 (Torrential Watershed of Schmittbach (Salzburg) - Analysis of Precipitation and Runoff). *BFW-Berichte* 129. pp. 101.
- Hasenauer, H., 1994. A single tree simulator for uneven-aged mixed Norway spruce, Scots pine and Common beech-Norway spruce stands. *Forstl. Schriftenreihe, Univ. für Bodenkultur, Wien.* 8, pp. 152.
- Hasenauer, H., Merganicova, K., Petritsch, R., Pietsch, S.A., Thornton, P.E., 2003. Validating daily climate interpolations over complex terrain in Austria. *Agric. For. Meteorol.* 119, 87–107.

- Hlásny, T., Barcza, Z., Barka, I., Merganičová, K., Sedmák, R., Kern, A., Pajtík, J., Balázs, B., Fabrika, M., Churkina, G., 2014. Future carbon cycle in mountain spruce forests of Central Europe: Modelling framework and ecological inferences. *For. Ecol. Manage.* 328, 55–68.
- Holland, E.A., Braswell, B.H., Lamarque, J.-F., Townsend, A., Sulzman, J., Müller, J.-F., Dentener, F., Brasseur, G., Levy II, H., Penner, J.E., Roelofs, G.-J., 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J. Geophys. Res.* 102, 15849–15866.
- Holland, E.A., Dentener, F.J., Braswell, B.H., Sulzman, J.M., 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry.* 46, 7–43.
- IPCC, 1992. *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment.* Cambridge University Press. pp. 200.
- IPCC, 2000. *Emission Scenarios: A Special Report of IPCC Working Group III.* Cambridge University Press. pp. 21.
- Iversen, C.M., Ledford, J., Norby, R.J., 2008. CO₂ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytol.* 179, 837–47.
- Johnson, D.W., Cheng, W., Joslin, J.D., Norby, R.J., 2004. Effects of elevated CO₂ on nutrient cycling in a sweetgum plantation. *Biogeochemistry* 69, 379–403.
- JRC - Forest Action, 2014. *Forest Ecosystem Services [WWW Document].* URL <http://forest.jrc.ec.europa.eu/activities/forest-ecosystem-services/> (accessed 23.3.15).
- Kilian, W., Müller, F., Starlinger, F., 1994. *Die forstlichen Wuchsgebiete Österreichs (The Forest Eco-regions of Austria).* BFW-Berichte. 82, pp. 60.
- Lautenschlager, M., Keuler, K., Wunram, C., Keup-Thiel, E., Schubert, M., Will, A., Rockel, B., Boehm, U., 2009a. Climate Simulation with CLM, Scenario A1B run no.1, Data Stream 3: European region MPI-M/MaD. World Data Center for Climate. doi: 10.1594/WDCC/CLM_A1B_1_D3, Hamburg.
- Lautenschlager, M., Keuler, K., Wunram, C., Keup-Thiel, E., Schubert, M., Will, A., Rockel, B., Boehm, U., 2009b. Climate Simulation with CLM, Scenario B1 run no.1, Data Stream 3: European region MPI-M/MaD. World Data Center for Climate. doi:10.1594/WDCC/CLM_B1_1_D3, Hamburg.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manage.* 259, 698–709.
- Little, E.L., 1971. *Atlas of United States trees, volume 1, conifers and important hardwoods.* U.S. Department of Agriculture.
- Medlyn, B.E., Duursma, R. a., Zeppel, M.J.B., 2011. Forest productivity under climate change: a checklist for evaluating model studies. *Wiley Interdiscip. Rev. Clim. Chang.* 2, 332–355.
- Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T., Johnson, D.W., 2002. Net Primary Productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecol. Appl.* 12, 1261–1266.
- Norby, R.J., Iversen, C.M., 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology.* 87, 5–14.
- Norby, R.J., Iversen, C.M., Ledford, J., Tharp, M.L., 2008. ORNL Net Primary Productivity Data. Carbon Dioxide Information Analysis Center (<http://cdiac.ornl.gov>), U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN.

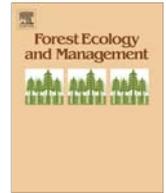
- Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E., O'Neill, E.G., 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO₂ enrichment. *Proc. Natl. Acad. Sci. U. S. A.* 101, 9689–93.
- Norby, R.J., Tharp, M.L., 2008. ORNL FACE Leaf Area Index (LAI) Data. Carbon Dioxide Information Analysis Center (<http://cdiac.ornl.gov>), U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN.
- Norby, R.J., Todd, D.E., Fulst, J., Johnson, D.W., 2001. Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytol.* 150, 477–487.
- Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., Mcmurtrie, R.E., 2010. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *PNAS.* 107, 19368–19373.
- Norby, R.J., Wullschlegel, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell Environ.* 22, 683–714.
- Obersteiner, E., Offenthaler, I., 2008. Critical Loads für Schwefel- und Stickstoffeinträge in Ökosysteme (Critical Loads for sulfur and nitrogen deposition in ecosystems). Environment Agency Austria (Umweltbundesamt), Vienna. pp. 58.
- Pallardy, S.G., 2008. *Physiology of Woody Plants*, 3rd ed. Academic Press, Amsterdam. pp. 454.
- Petritsch, R., 2002. Anwendung und Validierung des Klimainterpolationsmodells DAYMET in Österreich (Application and validation of the climate interpolation model DAYMET in Austria). Master thesis, University of Natural Resources and Life Sciences, Vienna. pp. 95.
- Petritsch, R., Hasenauer, H., 2007. Interpolating input parameters for large scale ecosystem models. *Austrian J. For. Sci.* 124, 135–151.
- Pietsch, S.A., Hasenauer, H., 2006. Evaluating the self-initialization procedure for large-scale ecosystem models. *Glob. Chang. Biol.* 12, 1658–1669.
- Pietsch, S.A., Hasenauer, H., 2009. Photosynthesis Within Large-Scale Ecosystem Models, in: Laisk, A., Nedbal, L., Govindjee (Eds.), *Advances in Photosynthesis and Respiration: Volume 29: Photosynthesis in Silico*. Springer, Dordrecht, pp. 441–464.
- Pietsch, S.A., Hasenauer, H., Thornton, P.E., 2005. BGC-model parameters for tree species growing in central European forests. *For. Ecol. Manage.* 211, 264–295.
- Placer, K., Schneider, J., 2001. Arbeiten zur Kartierung der trockenen Deposition in Österreich (Studies on the mapping of dry deposition in Austria). Environment Agency Austria (Umweltbundesamt). pp. 48.
- Pötzelberger, E., Hasenauer, H., 2015a. Forest–water dynamics within a mountainous catchment in Austria. *Nat. Hazards*. doi: 10.1007/s11069-015-1609-x
- Pötzelberger, E., Hasenauer, H., 2015b. Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests. *For. Ecol. Manage.* 338, 176–182.
- Pötzelberger, E., Wolfslehner, B., Hasenauer, H., 2015. Climate change impacts on key forest functions of the Vienna Woods. *Eur. J. For. Res.* doi: 10.1007/s10342-015-0866-2
- Reineke, L.H., 1933. Perfecting a stand density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- Richards, W.H., Koeck, R., Gersonde, R., Kuschnig, G., Fleck, W., Hochbichler, E., 2012. Landscape-scale Forest Management in the Municipal Watersheds of Vienna, Austria, and Seattle, USA: Commonalities Despite Disparate Ecology and History. *Nat. Areas J.* 32, 199–207.

- Saxe, H., Ellsworth, D.S., Heath, J., 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytol.* 139, 395–436.
- Schneider, J., 1998. Kartierung der nassen Deposition in Österreich (Mapping of the wet deposition in Austria). Environment Agency Austria. pp. 40.
- Seidl, R., Rammer, W., Lexer, M.J., 2011. Climate change vulnerability of sustainable forest management in the Eastern Alps. *Clim. Change* 106, 225–254.
- Thornton, P.E., 1998. Regional Ecosystem Simulation: Combining Surface- and Satellite-Based Observations to Study Linkages between Terrestrial Energy and Mass Budgets. PhD thesis, University of Montana, Missoula. pp. 280.
- Thornton, P.E., Hasenauer, H., White, M., 2000. Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric. For. Meteorol.* 104, 255–271.
- Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.* 113, 185–222.
- Thornton, P.E., Running, S.W., White, M., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251.
- Warren, J.M., Norby, R.J., Wullschleger, S.D., 2011a. Elevated CO₂ enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiol.* 31, 117–30.
- Warren, J.M., Pötzelsberger, E., Wullschleger, S.D., Thornton, P.E., Hasenauer, H., Norby, R.J., 2011b. Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂. *Ecohydrology.* 4, 196–210.
- Weiss, P., Schieler, K., Schadauer, K., Radunsky, K., Englisch, M., 2000. Die Kohlenstoffbilanz des österreichischen Waldes und Betrachtungen zum Kyoto-Protokoll (The carbon balance of the Austrian forests and consideration of the Kyoto protocol) - Monographien Band 106. Federal Environmental Agency, Austria. pp. 94.
- White, M., Thornton, P.E., Running, S.W., Nemani, R.R., 2000. Parameterization and Sensitivity Analysis of the BIOME-BGC Terrestrial Ecosystem Model: Net Primary Production Controls. *Earth Interact.* 4, 1–85.

APPENDIX

APPENDIX I

Pötzelsberger, E., Hasenauer, H., 2015. Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests. *For. Ecol. Manage.* 338, 176–182.



Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests



Elisabeth Pötzelberger*, Hubert Hasenauer

Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna, Peter-Jordan-Str. 82, A-1190 Vienna, Austria

ARTICLE INFO

Article history:

Received 25 August 2014

Received in revised form 25 November 2014

Accepted 26 November 2014

Keywords:

Forest management

Age class forest

Plenter forests

Norway spruce

Degradation

Soil recovery

ABSTRACT

Intensive forest management is known to influence soil structure and composition. Homogenous age class forests managed in a clear cut system reduce soil carbon and nutrients. Continuous cover forests (including plenter/single tree selection forests) on the other hand are considered to be a sustainable alternative, but little is known about their influence on soil carbon and soil nitrogen stocks. In this study, we investigated the recovery of soil carbon and nitrogen stocks after converting Norway spruce dominated age class forests (AC) into single tree selection/plenter forests (PL) at the Koralpe in the Austrian province of Styria. These forests originated from previous age class forests and the PL evolved after a decision from the early 1960s to change management from an age class system to a plenter system. Ten pairs of each a typical age class Norway spruce forest and a plenter forest adjacent to one another were obtained. The two stands of a pair are characterised by the same site conditions, and had the same stand history prior to the transition of one of the two stands. Differences in the stand and soil parameters by management regime are apparent. On the PL sites mineral soil in 0–20 cm depth contains 9 Mg C ha⁻¹ or 11% more carbon and 0.4 Mg N ha⁻¹ or 11% more nitrogen compared to the AC sites. Differences in total soil carbon (litter plus mineral soil) are not significant, whereas higher total soil nitrogen at PL are evident. These results suggest that soil conditions responded to changes in forest management practices.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

For centuries overexploitation of forest resources have resulted in forest and soil degradation and a shortage of timber supply across Europe (Glatzel, 1999). Large clear cuttings were continuously applied to address the emerging demand of timber mainly driven by the growing industrialization and population increase. Fast growing coniferous tree species such as Norway spruce (*Picea abies* [L.] Karst) were promoted in areas of mixed species stands but also on typical broadleaved sites (Spiecker et al., 2004).

Today, researchers suggest that these conifer-dominated age class forests are highly susceptible to biotic and abiotic disturbances, including storm, snow, drought, insects, fungi and soil degradation (Pommerening and Murphy, 2004; Spiecker et al., 2004). Thus a transformation of such even-aged plantations into diverse, uneven-aged single tree selection or so called plenter forests is currently pursued to address the sustainability requirements of forest management, including forest soils (Pommerening and Murphy, 2004).

Forest soils fulfil important ecosystem functions such as the storage of water and nutrients to sustain forest growth as well as

providing a habitat for soil microorganisms important for mineralisation and nutrient fixation processes (Blum, 2005). In recent years, forest soils have become a main focus in the context of carbon sequestration for mitigating climate change effects (Liski et al., 2002; Schulze and Freibauer, 2005). In temperate forests, average soil carbon stock is estimated to be 60% of the terrestrial carbon stock (Lal, 2005). Weiss et al. (2000) calculated the carbon stocks in Austrian forest soils at 0–50 cm depth to be 106 Mg C ha⁻¹.

Tree species, climate and bedrock fundamentally influence the development of soil structure and composition. Forest stand structure and succession dynamics alter light, temperature and moisture conditions as well as the input of dead organic material and drive soil processes. Forest management strongly affects such processes, particularly if the natural species composition has been changed and large forest clear cuttings are applied (Berger et al., 2002; Gautam et al., 2010; Pietsch and Hasenauer, 2002; Prietzel and Bachmann, 2012; Vesterdal et al., 2008). Other forest management impacts are (i) thinnings, which reduce total biomass and litter production as well as changes in microclimate (Jandl et al., 2007), (ii) whole tree harvesting (Johnson et al., 2002; Johnson and Curtis, 2001; Olsson et al., 1996) and the (iii) principal silvicultural management system (e.g. coppice with standards, clear cut, shelterwood, plenter system) (compare e.g. Laporte et al., 2003;

* Corresponding author. Tel.: +43 1 476544072; fax: +43 1 476544092.

E-mail address: elisabeth.poetzelsberger@boku.ac.at (E. Pötzelberger).

Bauhus et al., 2004; Bruckman et al., 2011). Thinnings and clear cuts have similar effects on the soil processes, but differ in intensity. Forest openings (e.g. removal of the canopy) change the temperature and water regime (Aussenac, 2000). This induces faster mineralisation processes (Binkley, 1984; Piene and Cleve, 1978), and reduces biomass production and thus leaf and root litter input to the soil (Jandl et al., 2007; Skovsgaard et al., 2006). A long history of clear cuts and intensive use of forest biomass has reduced productivity due to soil carbon and nutrient loss in the Alpine region (Bochter et al., 1981; Glatzel, 1999; Pietsch and Hasenauer, 2002). In a recent meta-analysis covering more than 400 studies, Nave et al. (2010) concluded that overall harvesting operations and particularly large clear cut systems result in a significant reduction in the soil C storage of the forest floor.

Historically speaking, clear cutting was the main forest management system leading to the reported degradation effects (Spiecker et al., 2004). The clear cut system also led to pure even-aged forest stands due to their uniform light regime, which promotes the regeneration of light demanding tree species (Burschel and Huss, 2003; Mayer, 1999). As an alternative, continuous cover forestry systems, which avoid clear cutting and include the single tree selection or so called plenter forest system, are widely discussed (Hasenauer and Sterba, 2000; Pommerening and Murphy, 2004; Zingg et al., 1997). The principle idea of this management system is that small openings in the canopy (e.g. gaps) mimic the natural succession dynamics of forest stands more realistically and thus no or only minor degradation effects are evident. This is because little or no changes in the soil surface and in microclimate are evident and continuous litter input is provided (Vesterdal and Leifeld, 2007). Additionally we can assume that the light conditions within a forest stand may be used more effectively by different tree species or individual trees, since the ecological niches within a forest stand are utilised more efficiently (Binkley et al., 2013; Jandl, 2007; Pretzsch, 2014; Sterba, 2000). This improves growing conditions by avoiding degradation effects. Due to a more effective utilization of the available growing space, it may also lead to higher productivity rates as compared to the clear cut system (O'Hara et al., 2007).

Although several studies have investigated potential differences in long term timber production between a clear cut versus a continuous cover or plenter system (Kern, 1966; Mitscherlich, 1963; O'Hara et al., 2007), little is known about the effects on soils following changes in the management system from a previous clear cut system to a continuous cover single tree selection or plenter system. The objective of this study was to investigate the differences in soil carbon and nitrogen stocks by management system. We compared the differences in the soil C and N stocks of 10 pairs, each consisting of a pure even-aged Norway spruce forest (age class forest, AC) and a neighbouring single tree selection forest (plenter forest, PL), 50 years after the management regime of the PL was changed from clear cutting to single tree selections. We were specifically interested in finding out if a potential recovery of the soil, expressed as changes in the (i) mineral soil and (ii) litter layer of (iii) carbon, and (iv) nitrogen stocks, is detectable.

2. Material and methods

2.1. Study area

The investigated forests are owned by the forest enterprise 'Forstbetrieb Ligist, Souveräner Malteser Ritterorden' located in the western Styrian foothills in the mountain range Koralpe (highest peak 2140 m a.s.l.), Austria. The metamorphic, crystalline rock of the Koralpe consists of gneiss ('Stainzer Platten', gneissic banding) and schist but weathered hillside rock can be found in the area

as well (GIS-Steiermark, 2013). The soil type is podzolic cambisol. The potential natural vegetation in this middle-montane zone (900–1300 m a.s.l.) is a mixed Norway spruce-silver fir-European beech forest (forest growth district 5.4 West-Styrian Mountains) (Kilian et al., 1994). The average annual temperature is 6.5 °C. Mean annual precipitation is 1000 mm with a peak in the summer months. High precipitation rates in May and September indicate the climate transition zone between temperate and Mediterranean climate. A high frequency of thunderstorms and heavy precipitation events are also typical for the area.

Since 1928 the forest company has owned 900 ha of forests in the study region (Matzer, 2011). For almost three centuries, these forests were managed as Norway spruce (*P. abies* L. Karst) dominated age class forests (AC). Until the early 20th century they were harvested with large scale clear cuts of up to 20 ha or more. In the early 1960s, the management system was changed to single-tree selection (PL) promoting stand structure, species mixture and natural regeneration (about 90% of the forest area). Especially tree species such as silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) are supported (Matzer, 2011; Thurnher et al., 2011).

2.2. Study design

The principle objective of the study was to compare the soil carbon and nitrogen stocks of pairs of adjacent forest stands with different forest management. We selected 10 pairs of forest stands, one covering the typical characteristics of AC (age class forest managed as clear cuts) and one covering a typical PL (plenter forest or single tree selection forest). Historic records, provided by the forest enterprise, describe the historic management as age class forests until the 1960s (Spörk, 2011, personal communications, Thurnher et al., 2011); over the last 50 years large parts of the forest have gradually been transformed from the even-aged Norway spruce forests into plenter forests. This transformation process is still ongoing (Spörk, 2011, personal communications, Thurnher et al., 2011), yielding a mixture of AC and PL in the enterprise's forests. The location of the two stands of a pair (one AC, one PL) had to be in the same forest management unit (dt. 'Abteilung'). This approach assumes that the starting conditions – although no stand and soil data are available – were comparable 50 years ago and that the differences in the soil layers are management induced effects after 50 years of transformation. Since the selection of the pairs is essential for the study, the pairs (AC versus PL) had to be within a distance of less than 200 m and at the same site conditions, geology, elevation, slope, as well as aspect. The elevation of the selected forest sites ranged from 920 to 1160 m a.s.l. (Table 1).

In every forest stand we established a 15 m × 15 m sampling plot. Skidding trails and large canopy openings were avoided. We randomly selected the location of the north eastern corner of the north oriented plots. We took the soil samples 1 m clockwise from the corners. In case of trunks, stems, big tree roots or rocks, we shifted the sampling spot 15–175 cm clockwise. We collected the forest floor/litter layer in a 17.5 cm × 25.5 cm frame and removed living understorey vegetation. The mineral soil we sampled with a stainless steel root auger with a sampling cylinder of 15 cm in length and an inner diameter of 8 cm. The cylinder was repeatedly hammered into the soil at the same spot and the soil cores were separated so that we obtained the layers 0–20 cm, 20–50 cm and more than 50 cm in depth. The respective layers from the four corners were mixed.

2.3. Forest stand data

Forest stand data were recorded using four angle count samples (Bitterlich, 1948) per stand, located at every corner. A basal area factor of 4 was used (so each tree in the sample represents a basal

Table 1
Mean, minimum (Min), maximum (Max) and standard deviation (S_d) of (i) the site characteristics elevation, slope and aspect as well as (ii) the stand characteristics tree volume, basal area, stem number, mean height, dominant height (height of the 3 thickest trees within an angle count sample using the basal area factor of 4), quadratic mean diameter and yield class (mean annual volume increment at age 100 according to Marschall (1975)).

	Age class forest (AC)				Plenter forest (PL)			
	Mean	Min	Max	S_d	Mean	Min	Max	S_d
Elevation (m)	1042	925	1162	84	1041	920	1155	87
Slope (°)	10.9	5.7	18.0	4.2	11.0	6.8	14.8	2.7
Aspect	N-E	N	S-E	–	N-E	N	S-E	–
Volume ($m^3 ha^{-1}$)	498	343	642	106	563	330	849	166
Basal area ($m^2 ha^{-1}$)	45.1	34.0	55.0	7.7	44.5	27.0	62.0	12.0
Stem number (ha^{-1})	1118	520	1687	290	975	137	2035	541
Mean tree height (m)	23.5	21.0	25.4	1.3	29.2	24.2	36.7	3.8
Dominant tree height (m)	28.3	24.7	30.6	1.8	35.8	28.1	38.2	3.2
Quadratic mean diameter (cm)	23	19	29	3	27	19	50	9
Yield class (Marschall, 1975)	9.3	8.7	10.0	0.5	9.3	8.7	10.0	0.5

area of $4 m^2 ha^{-1}$). Tree species, height and DBH of all the trees in the angle count sample points with a minimum diameter of 60 mm were recorded. We then calculated stand volume, basal area, number of trees, mean tree height, dominant tree height, quadratic mean diameter, Shannon index and Evenness. Volume was calculated using the form factor function of Pollanschütz (1974). Dominant tree height is the height of the trees with the largest diameter for which the sum of the basal area is $12 m^2$. Hence, in our case of angle count samples with a basal area factor of 4, the three trees with the largest diameter were taken. The quadratic mean diameter was calculated from the mean individual tree basal area.

Yield class defined as the mean annual increment at age 100 (Marschall, 1975) was obtained from the company's forest management plan. Shannon index H' , a measure for the number of species s and their even distribution based on the volume proportion of the species p_i was calculated as:

$$H' = -\sum_{i=1}^s p_i \cdot \ln p_i. \quad (1)$$

Evenness E indicates the even distribution of the species within mixed species forests and was calculated as:

$$E = \frac{H'}{\ln s} \quad (2)$$

2.4. Soil analysis

The forest floor was oven-dried at 60 °C, weighed, cut into smaller pieces using a knife mill and finely milled with a ball mill. We equally split the fresh mineral soil samples into two to three subsamples, depending on the amount of soil and weighed them. Immediately after weighing we sieved a randomly chosen subsample to 2 mm and manually removed roots and other coarse organic materials (hereafter only called roots). Rocks and roots were washed, dried at 60 °C and weighed. Immediately after sieving three times 10 g of the fine soil (< 2 mm) were taken; two times 10 g were dried at 60 °C and 10 g at 105 °C to constant mass and weighed. With this information we calculated the water content of the fresh fine soil relative to the 60 °C and 105 °C dry soil. For the roots we assumed the same water content as for the fresh soil relative to the 60 °C dry fine soil. We used the fresh weight of the roots and the weight of the rocks to calculate the weight content (%) of roots and of rocks in the fresh subsample. We calculated the fine soil dry (105 °C) mass by reducing the weight of the fresh sample by the content of roots and rocks and the water content of the fresh fine soil relative to the 105 °C dry soil. 10 g of soil dried at 60 °C were fine-milled in a ball mill. Carbon and nitrogen concentration of the finely milled mineral soil and litter samples were

measured with a Perkin–Elmer PE 2400 Series II CHNS/O elemental analyzer. The C and N concentration was recalculated to give the C and N concentration in 105 °C dry soil ($g kg^{-1}$). We used the fine soil dry mass, the C and N concentration in the fine soil and the horizontal surface area of the soil auger to calculate the C and N stocks ($Mg ha^{-1}$) for each soil layer. We then calculated C and N stocks ($Mg ha^{-1}$) from the dry litter mass, the C and N concentration in the litter and the horizontal surface area of the litter frame. The C/N ratio was derived from the ratio between C and N concentrations.

The pH was determined for the layer 0–20 cm from one corner per sampling plot for half of the pairs. The pH was measured with a 'pH 192' (WTW company) in 0.01 M $CaCl_2$ after an equilibrium time of 24 h following the instructions for the Austrian soil inventory (Blum et al., 1996).

3. Analysis and results

3.1. Site and stand characteristics

We started our analysis by comparing the common site and stand characteristics for each of the selected 10 pairs of forest stands composed of (i) 10 stands managed as an age class clear cut system (AC) and (ii) 10 stands in transition towards a plenter forest (PL). The two stands for each pair (AC, PL) were located next to each other to ensure that they were identical in stand management history (until 1960) and in site conditions. The dominating exposition is North-East, with one pair being north oriented and one pair being South-East oriented. Average slope for AC as well as the PL plots is 11 degrees and no differences in elevation are evident, confirming that the sites by pair are comparable (Table 1).

The stand characteristics volume, basal area, number of trees, mean tree height, dominant tree height, quadratic mean diameter and yield class according to Marschall (1975) for AC and PL are also provided in Table 1. Any differences in the numbers are due to the changes in the management system between the early 1960s and now. Both forest types are dominated by Norway spruce. However, for PL the volume proportion of the Norway spruce has declined to about 60%, while silver fir, larch and beech have increased their share versus the AC plots (see Table 2). Next, we assessed the species diversity indicators Shannon index and Evenness. The Shannon index is a measure for species diversity and the Evenness is an indicator for species distribution, where 1 indicates an equal distribution and values approaching 0 mean unequal distribution. Both indicators tended to be higher on untransformed plenter forests (Table 2). Fig. 1 provides a typical example of neighbouring/paired stands representing the situation of AC (mono-layered) versus PL (structure-rich).

Table 2

Mean species proportions by total stand volume including the Shannon and Evenness index for the 10 selected age class forest (AC) and the 10 plenter forest (PL) 50 years after the conversion process from an age class forests towards a continuous cover forest management has started. The Shannon index is as a measure of species diversity that increases with the number of species and the more equal distribution of the species, the Evenness index ranging from 0 to 1 expresses distribution of the species, with 1 for an equal distribution and approaching 0 for very unequal distribution.

Tree species	Age class forest (AC)	Plenter forest (PL)
<i>Picea abies</i> (Norway spruce)	74	61
<i>Abies alba</i> (silver fir)	12	18
<i>Pinus sylvestris</i> (Scots pine)	8	5
<i>Larix decidua</i> (European larch)	4	9
<i>Acer pseudoplatanus</i> (Sycamore maple)	2	0
<i>Fagus sylvatica</i> (European beech)	1	7
Shannon index	0.93	1.16
Evenness	0.52	0.72

3.2. Mineral soil and litter

The soil carbon and soil nitrogen pools are strongly affected by forest management (Jandl et al., 2007; Johnson and Curtis, 2001; Pietsch and Hasenauer, 2002). For our data we hypothesize that the 50 years of transformation of an age class forest into a plenter forest may result in a difference of forest soil carbon and nitrogen pools between AC and PL.

For the soil C and N analysis we split the soil data into the litter layer and the following mineral soil layers: (i) 0–20 cm soil depth, (ii) 20–50 cm and (iii) below 50 cm soil depth. Forest management changes immediately affect the litter layer, whereas any reaction in the mineral soil layers will have a time lag effect but are more important for the long term storage effect. We investigated the C and N concentration, C and N stocks and the C/N ratio at the different soil depths. The C and N concentrations are defined as the weight content of C and N in the oven dry fine soil (g C or N per kg dry matter). The actual C and N stocks in the soil (Mg ha^{-1}) vary with the rock and root content and the soil density. The C/N is the C and the N concentration ratio. Soil carbon stems from litter and fine roots, whereas nitrogen enters the soil through atmospheric deposition, biological fixation and litter. Carbon mainly leaves the soil through respiration; however C can also be lost through leaching along with nitrogen; and nitrogen can be lost through volatilisation. The C/N ratio summarises the history of C and N input and loss and is seen as an indicator of N availability (Bruckman et al., 2011).

For each variable – (i) C and N concentration, (ii) C and N stocks and (iii) C/N ratio for litter and the three mineral soil layers – we calculated the mean of the four samples per stand. From these stand values we derived the mean and standard deviation per

forest management type (the 10 AC and the 10 PL) for each variable. Fig. 2 and Table 3 provide the mean and the standard deviation for all variables by management type. In addition Table 3 gives the minimum and maximum values for the selected soil parameters.

For each of the 10 pairs i we calculated the differences Δ_i of PL_i and AC_i for each of the soil parameters:

$$\Delta_i = PL_i - AC_i \quad (3)$$

To test for significance we used the paired t -statistics:

$$t = \frac{\bar{\Delta}_i}{Sd_{\Delta}} \sqrt{n} \quad (4)$$

where t is the t -value of the paired t -statistics, $\bar{\Delta}$ is the mean of the differences of PL and AC, n is the number of pairs and Sd_{Δ} is the standard deviation of the differences. Table 3 provides the mean of the differences between PL and AC, the standard deviation of the differences and the results of the t -statistics for each soil parameter.

Soil pH was also determined for AC and PL. The mean pH in 0–20 cm soil depth on the AC stands is 3.68 and 3.47 for the PL sites.

4. Discussion and conclusions

50 years after changing the management system from an age class clear cut management system to a continuous cover single tree selection or plenter system, differences in the carbon and nitrogen stocks are evident (Fig. 2). Carbon stocks in the upper mineral soil layer (0–20 cm) on PL sites with 92 Mg C ha^{-1} are significantly higher versus AC sites with 82 Mg C ha^{-1} ($\Delta_i = 9 \text{ Mg C ha}^{-1}$ or 11%, $t = 2.34 > t_{\alpha = 0.025, N = 10} = 2.26$) (Table 3). For the other soil layers, the carbon stocks tend to be higher on PL sites but no significant differences are noticeable. Significantly higher nitrogen stocks are evident on the PL sites. Total nitrogen stocks at the upper mineral soil layer (0–20 cm) are 3.9 Mg N ha^{-1} on the PL sites and 3.6 Mg N ha^{-1} for the AC (11% higher nitrogen stocks for PL than AC). In the lower mineral soil layer (20–50 cm) we found 2.1 Mg N ha^{-1} on the PL sites versus 1.9 Mg N ha^{-1} on the AC. Total nitrogen stocks (mineral soil plus litter layer, 6.8 Mg N ha^{-1} on the PL versus 6.1 Mg N ha^{-1} on the AC sites) were significantly higher at PL than at AC ($\Delta = 0.6 \text{ Mg N ha}^{-1}$, $t = 2.7 > t_{\alpha = 0.025, N = 10} = 2.26$).

For the litter layer no significant differences in the carbon and nitrogen concentrations and stocks were found between AC and PL. Large canopy gaps following management interventions, such as intensive thinning, can reduce leaf litter input temporarily (Hager, 1988; Skovsgaard et al., 2006; Vesterdal et al., 1995) until the full canopy closure is regained (Vesterdal et al., 1995). In the investigated forests, stand density was relatively high (Table 1)



Fig. 1. Typical situation of the investigated pairs of forest stands. Left: the age class forest, dominated by Norway spruce, managed since more than 300 years in rotation clear cut system (AC). Right: the stand situation 50 years after the conversion process from a previous age class forest dominated with Norway spruce and managed in the clear cut system towards a continuous cover single tree selection or plenter forest (PL) has started.

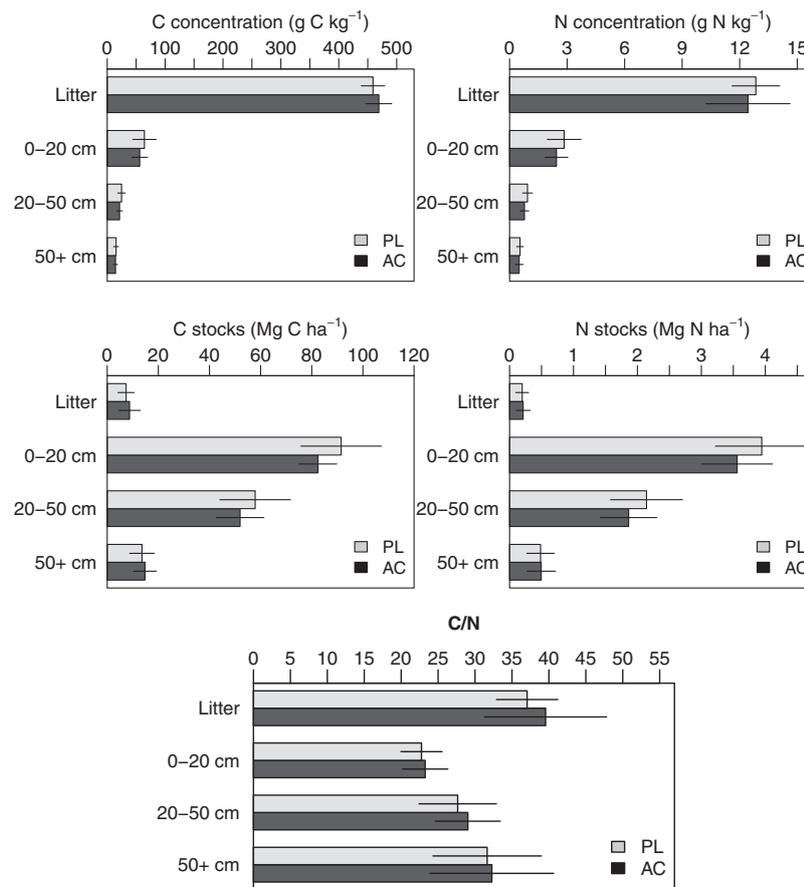


Fig. 2. Mean and standard deviation for carbon and nitrogen concentration (C and N in g kg⁻¹ dry fine soil), the carbon and nitrogen stocks (C and N in Mg ha⁻¹) and the carbon to nitrogen ratio (C/N) in the litter and the three mineral soil layers (0–20 cm; 20–50 cm; 50+ cm) of the 10 age class forests (AC) versus the 10 plenter forests (PL) 50 years after the conversion process has started.

and no large canopy gaps were evident. The high variability among the forest stands by management regime with a standard deviation in the litter C and N stocks of around 50% (Table 3) makes potential differences difficult to detect.

Changes in the mineral soil C and N stocks did not translate into significant changes in the C/N ratios (Table 3). This suggests that differences in the litter quality (litter inherent C/N ratio), which may result from tree species changes, are not evident. Humification of soil organic matter leads to the oxidation of carbon and to the relative accumulation of soil nitrogen and thus a narrower C/N ratio, often observed in deeper soil layers (Bruckman et al., 2011). However, the observed relatively high C/N ratio in the mineral soil, more pronounced in deeper soil layers for both AC and PL, is typical for acidified soils (Blume et al., 2010). Indeed, soil pH is very low, with around 3.5 for both AC and PL. Thus, soil quality indicated by C/N or pH does not show an improvement 50 years after the shift in management.

A key prerequisite for the detection of management induced differences in soil carbon and nitrogen stocks are comparable initial conditions and comparable site conditions. Prior to the early 1960s, both current AC and PL were managed as clear cut forests, before the forest enterprise decided to change the forest management towards a continuous cover, single tree selection forest system. In addition, the stands of a pair are found within a distance of less than 200 m and at the same elevation, slope as well as exposition. This ensures that the initial conditions – although no measurement data are available – are comparable and that the differences in the soil layers are only management induced. Note that this approach also ensures that any external long-term

impacts within the region (e.g. climate change effects, N deposition rates, etc.) (Schulze and Freibauer, 2005) have affected both AC and PL stands. The shift in the management system caused that PL are characterised by a second or third canopy layer today, whereas AC are still mono-layered (see Fig. 1). This is expressed in a larger differentiation (higher standard deviation) of the tree height in PL (Table 1). The higher Evenness of the PL suggests that the transformation from a Norway spruce dominated age class forest to a more diverse selection forest (compare Table 2) is ongoing. However, since the conversion process started, no clear cuts with major impacts on soil C and N stocks have been applied on the AC plots. Thinning interventions have been performed, which also impact soil C stocks (Jandl et al., 2007). We regard single tree extractions in structured multi-layer forest stands as having a lower negative impact on the soil versus stand wise thinnings in homogenous age class forests. An increased growth of the relieved second or third tree layer of a PL with a higher species diversity (Table 2) can compensate for production loss in the upper canopy layer (Pretzsch, 2014). It closes canopy gaps faster and stabilises the microclimate and therefore decomposition. The hypothesis of little negative impact on the soil by selective harvesting is also confirmed by a study in the Bavarian Limestone Alps (Christophel et al., 2013) where no reductions in mineral soil C and N at 0–30 cm depth due to single tree harvesting compared to unmanaged natural forests were detectable. The 11% higher storage of C and N in the mineral soil at 0–20 cm in PL versus AC in this study (Table 3) is an indication of an ameliorative effect of the conversion of the management system from AC to PL. Today single tree selection forests with high structural diversity, a higher (native) species

Table 3

Mean, minimum (Min), maximum (Max) and standard deviation (S_d) of carbon and nitrogen concentration (C and N g kg⁻¹), the carbon and nitrogen stocks (C and N Mg ha⁻¹) and carbon to nitrogen ratio (C/N) for the age class forests and plenter forests plus the difference Δ and the standard deviation $S_{d,\Delta}$ between the PL and AC forest stands. The t -value was calculated as a paired t -statistics and the significant values are * for $\alpha = 0.05$, and ** significant for $\alpha = 0.01$.

Variable	Layer	Age class forest (AC)				Plenter forest (PL)				$\Delta = \bar{P}L_i - \bar{A}C_i$			
		Mean	Min	Max	S_d	Mean	Min	Max	S_d	Δ	$S_{d,\Delta}$	n	t -Value
[C] (g C kg ⁻¹)	Litter	469	434	500	22	459	432	501	20	-10	18	10	-1.83
	0–20 cm	56	42	86	14	64	33	90	20	8	18	10	1.85
	20–50 cm	21	12	29	5	25	16	37	6	4	4	10	2.44*
	50+ cm	14	9	20	3	15	10	21	4	1	4	10	0.79
[N] (g N kg ⁻¹)	Litter	12.4	8.4	15.8	2.2	12.8	11.3	14.9	1.2	0.4	2.1	10	0.62
	0–20 cm	2.4	1.8	3.6	0.6	2.8	1.8	3.9	0.9	0.4	0.6	10	2.21
	20–50 cm	0.8	0.5	1.2	0.2	0.9	0.6	1.4	0.3	0.2	0.1	10	3.82**
	50+ cm	0.5	0.2	0.9	0.2	0.5	0.3	0.9	0.2	0	0.1	10	1.2
C stocks (Mg C ha ⁻²)	Litter	9	4	16	4	7	3	14	3	-1	4	10	-1.08
	0–20 cm	82	72	98	7	92	66	118	16	9	4	10	2.34*
	20–50 cm	52	36	66	9	58	36	80	14	6	10	10	1.82
	50+ cm	15	8	22	4	14	7	24	5	-1	2	10	-1.67
	0–50 cm	134	111	164	15	149	116	197	28	15	21	10	2.23
	Litter-50+ cm	158	133	188	18	170	134	217	32	12	24	10	1.53
N stocks (Mg N ha ⁻²)	Litter	0.2	0.1	0.4	0.1	0.2	0.1	0.4	0.1	0	0.1	10	-0.55
	0–20 cm	3.6	2.5	4.3	0.6	3.9	3.1	5.1	0.7	0.4	0.1	10	2.25
	20–50 cm	1.9	1.3	2.8	0.4	2.1	1.5	3.3	0.6	0.3	0.3	10	3.15*
	50+ cm	0.5	0.2	1	0.2	0.5	0.2	1	0.2	0	0.1	10	-0.36
	0–50 cm	5.4	3.8	6.9	0.9	6.1	4.7	8.4	1.2	0.7	0.7	10	2.97*
	Litter-50+ cm	6.1	4.2	8.3	1.1	6.8	5.3	9.8	1.4	0.6	0.7	10	2.7*
C/N	Litter	40	30	58	8	37	30	44	4	-2	8	10	-1
	0–20 cm	23	20	30	3	23	18	27	3	0	3	10	-0.59
	20–50 cm	29	24	36	4	28	18	36	5	-1	3	10	-1.38
	50+ cm	32	22	52	8	32	20	42	7	-1	6	10	-0.31

diversity and continuous forest cover that never exposes the soil are widely considered stable, sustainable systems (Pommerening and Murphy, 2004). Traditional sustainability indicators used to describe plenter systems are stand density, tree species diversity, basal area increment and stand structure (O'Hara et al., 2007). However, current sustainability discussions in the forestry field certainly call for the inclusion of soil carbon and nitrogen storage into the set of sustainability indicators, although changes in soil conditions are difficult to track due to high spatial variability. The differences between AC and PL and the mineral soil C and N stocks presented show that forest soils react to changes in forest management, only 50 years after the conversion from AC to PL was initiated. This suggests that the continuous forest cover in a single tree selection forest has the potential to increase the mineral soil carbon and nitrogen stocks. Thus, changes in forest management practices have the potential to ameliorate soils degraded by historical impact of the clear cut system.

Acknowledgements

We thank Univ. Prof. Dr. Josef Spörk, the retired Professor for Silviculture, University of Natural Resources and Life Sciences and the former manager of the forest company, for giving the motivation to the study. We also thank Dipl.-Ing. Clemens Spörk, the forest manager of the 'Forstbetrieb Ligest, Souveräner Malteser Ritterorden' for providing the technical and financial support for the fieldwork. Thanks to Univ. Doz. Dr. Franz Zehetner for helping with the technical soil sampling design. Thanks also to Mag. Christian Quehenberger and Dipl.-Ing. Mario Matzer for their support in the fieldwork.

References

Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* 57, 287–301.

- Bauhus, J., Vor, T., Bartsch, N., Cowling, A., 2004. The effects of gaps and liming on forest floor decomposition and soil C and N dynamics in a *Fagus sylvatica* forest. *Can. J. For. Res.* 34, 509–518.
- Berger, T.W., Neubauer, C., Glatzel, G., 2002. Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (*Picea abies*) and mixed species stands in Austria. *For. Ecol. Manage.* 159, 3–14.
- Binkley, D., 1984. Does forest removal increase rates of decomposition and nitrogen release? *For. Ecol. Manage.* 8, 229–233.
- Binkley, D., Laclau, J.-P., Sterba, H., 2013. Why one tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. *For. Ecol. Manage.* 288, 1–4.
- Bitterlich, W., 1948. Die Winkelzählprobe (the angle-count sample). *Allg. Forst – Holzwirtschaftszeitung* 59, 4–5.
- Blum, W.E.H., 2005. Functions of soil for society and the environment. *Rev. Environ. Sci. Bio/Technol.* 4, 75–79.
- Blum, W.E.H., Spiegel, H., Wenzel, W.W., 1996. Bodenzustandsinventur. Konzeption, Durchführung und Bewertung (Soilinventory), second ed. Institute of Soil Research, University of Natural Resources and Life Sciences, Vienna.
- Blume, H.-P., Brümmer, G.W., Horn, R., Kandelner, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., Wilke, B.-M., 2010. Scheffer/Schachtschabel Lehrbuch der Bodenkunde, 16th ed. Spektrum Akademischer Verlag, Heidelberg.
- Bochter, R., Neuberger, W., Zech, W., 1981. Humus und Humusschwund im Gebirge (Humus and humus loss in the mountains), in: Nationalpark Berchtesgaden. Forschungsberichte 2. Nationalparkverwaltung Berchtesgaden.
- Bruckman, V.J., Yan, S., Hochbichler, E., Glatzel, G., 2011. Carbon pools and temporal dynamics along a rotation period in *Quercus* dominated high forest and coppice with standards stands. *For. Ecol. Manage.* 262, 1853–1862.
- Burschel, P., Huss, J., 2003. Grundriss des Waldbaus (Outline of silviculture), third ed., Ulmer.
- Christophel, D., Spengler, S., Schmidt, B., Ewald, J., Prietzel, J., 2013. Customary selective harvesting has considerably decreased organic carbon and nitrogen stocks in forest soils of the Bavarian Limestone Alps. *For. Ecol. Manage.* 305, 167–176.
- Gautam, S., Pietsch, S.A., Hasenauer, H., 2010. Modelling thinning response in coppice versus high oak forests in Austria. *Austrian J. For. Sci.* 127, 179–201.
- GIS-Steiermark, 2013. Digitaler Atlas der Steiermark. Geologie & Geotechnik [WWW Document]. <[http://gis2.stmk.gv.at/atlas/\(S\(d2rry1qztr2wpdigoam5f5xd\)\)/init.aspx?karte=erdwiss&ks=das&cms=da&massstab=800000&t=635322088124428372](http://gis2.stmk.gv.at/atlas/(S(d2rry1qztr2wpdigoam5f5xd))/init.aspx?karte=erdwiss&ks=das&cms=da&massstab=800000&t=635322088124428372)> (accessed 4.4.14).
- Glatzel, G., 1999. Historic forest use and its possible implication to recently accelerated tree growth in Central Europe. In: Karjalainen, T., Spieker, H., Laroussine, O. (Eds.), Causes and Consequences of Accelerated Tree Growth in Europe. *EFI Proceedings No. 27*, pp. 65–74.
- Hager, H., 1988. Stammzahlreduktion. Die Auswirkungen auf Wasser-, Energie- und Nährstoffhaushalt von Fichtenjungwüchsen (Precommercial thinning. The effects upon water, energy and nutrient household of sapling stands of Norway spruce). *Forstliche Schriftenreihe*. University of Natural Resources and Life Sciences, Vienna.

- Hasenauer, H., Sterba, H., 2000. The research program for the restoration of forest ecosystems in Austria. In: Klimo, E., Hager, H., Kulhavy, J. (Eds.), *Spruce Monocultures in Central Europe. Problems and Prospects*. European Forest Institute Proceedings NO. 33, pp. 45–52.
- Jandl, R., 2007. Carbon sequestration and forest management. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* 2.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137, 253–268.
- Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. *For. Ecol. Manage.* 140, 227–238.
- Johnson, D., Knoepp, J., Swank, W., Shan, J., Morris, L., Van Lear, D., Kapeluck, P., 2002. Effects of forest management on soil carbon: results of some long-term resampling studies. *Environ. Pollut.* 116, S201–S208.
- Kern, K.G., 1966. Wachstum und Umweltfaktoren im Schlag- und Plenterwald (Growth and environmental conditions in clear cut and plenter forests). Schriftenreihe der Forstlichen Abteilung der Universität Freiburg im Breisgau.
- Kilian, W., Müller, F., Starlinger, F., 1994. Die forstlichen wuchsgebiete österreichs (the forest ecoregions of Austria). *BFW-Berichte* 82, 60.
- Lal, R., 2005. Forest soils and carbon sequestration. *For. Ecol. Manage.* 220, 242–258.
- Laporte, M.F., Duchesne, L.C., Morrison, I.K., 2003. Effect of clearcutting, selection cutting, shelterwood cutting and microsites on soil surface CO₂ efflux in a tolerant hardwood ecosystem of northern Ontario. *For. Ecol. Manage.* 174, 565–575.
- Liski, J., Perruchoud, D., Karjalainen, T., 2002. Increasing carbon stocks in the forest soils of western Europe. *For. Ecol. Manage.* 169, 159–175.
- Marschall, J., 1975. *Hilfstafeln für die Forsteinrichtung (Yield tables for forest planning)*. Österreichischer Agrarverlag.
- Matzer, M., 2011. Einfluss der Waldbewirtschaftung auf die Kohlenstoffvorräte im Boden – Ein Vergleich zwischen Dauerwald und Altersklassenwald im Revier Sommereben, Weststeiermark (Impact of forest management on soil carbon stocks). Master Thesis, University of Natural Resources and Life Sciences, Vienna.
- Mayer, H., 1999. *Waldbau auf soziologisch-ökologischer Grundlage (Silviculture based on sociological and ecological principles)*, fourth ed. Spektrum Akademischer Verlag.
- Mitscherlich, G., 1963. Untersuchungen in Schlag- und Plenterwäldern (Investigations in clear cut and plenter forests). *Allg. Forst – Jagdzeitung* 134, 1–12.
- Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. *For. Ecol. Manage.* 259, 857–866.
- O'Hara, K.L., Hasenauer, H., Kindermann, G., 2007. Sustainability in multi-aged stands: an analysis of long-term plenter systems. *Forestry* 80, 163–181.
- Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., Kaj, R., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. *For. Ecol. Manage.* 82, 19–32.
- Piense, H., Cleve, K.Van, 1978. Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. *Can. J. For. Res.* 8, 42–46.
- Pietsch, S.A., Hasenauer, H., 2002. Using mechanistic modeling within forest ecosystem restoration. *For. Ecol. Manage.* 159, 111–131.
- Pollanschütz, J., 1974. Formzahlfunktionen der Hauptbaumarten Österreichs (Form factor functions of the main tree species in Austria). *Allg. Forstzeitung* 85, 341–343.
- Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77, 27–44.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manage.* 327, 251–264.
- Prietzl, J., Bachmann, S., 2012. Changes in soil organic C and N stocks after forest transformation from Norway spruce and Scots pine into Douglas fir, Douglas fir/spruce, or European beech stands at different sites in Southern Germany. *For. Ecol. Manage.* 269, 134–148.
- Schulze, E.-D., Freibauer, A., 2005. Carbon unlocked from soils. *Nature* 437, 11–12.
- Skovsgaard, J.P., Stupak, I., Vesterdal, L., 2006. Distribution of biomass and carbon in even-aged stands of Norway spruce (*Picea abies* (L.) Karst.): a case study on spacing and thinning effects in northern Denmark. *Scand. J. For. Res.* 21, 470–488.
- Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H., von Teuffel, K. (Eds.), 2004. *Norway Spruce Conversion – Options and Consequences*, European Forest Institute Research Report. Brill Academic Pub, Boston, Köln.
- Sterba, H., 2000. Uneven-aged forest management, does it combine sustainability and productivity? In: Jandl, R., Devall, M., Khorchidi, M., Schimof, E., Wolfrum, G., Krishnapillay, B. (Eds.), *Forests and Society: The Role of Research*. XXI IUFRO World Congress 2000, Abstracts of Group Discussions, vol. 11.
- Thurnher, C., Klopff, M., Hasenauer, H., 2011. *Forests in transition: a harvesting model for uneven-aged mixed species forests in Austria*. *Forestry* 84, 517–526.
- Vesterdal, L., Leifeld, J., 2007. Land-use change and management effects on soil carbon sequestration: Forstry and agriculture. In: Jandl, R., Olsson, M. (Eds.), *Greenhouse-Gas Budget of Soils under Changing Climate and Land Use (Burnout)*. COST Action 639. BFW – Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, pp. 25–32.
- Vesterdal, L., Dalsgaard, M., Felby, C., Raulund-rasmussen, K., Jørgensen, B.B., 1995. Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. *For. Ecol. Manage.* 77, 1–10.
- Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *For. Ecol. Manage.* 255, 35–48.
- Weiss, P., Schieler, K., Schadauer, K., Radunsky, K., Englisch, M., 2000. *Die Kohlenstoffbilanz des österreichischen Waldes und Betrachtungen zum Kyoto-Protokoll (The carbon balance of the Austrian forests and consideration of the Kyoto protocol) – Monographien, Band 106*. Federal Environmental Agency, Austria.
- Zingg, A., Erni, V., Mohr, C., 1997. Selection forests – a concept for sustainable use: 90 years of experience of growth and yield research selection forestry in Switzerland. In: Emmingham, W.H. (Ed.), *Proceedings of the IUFRO Interdisciplinary Uneven-Aged Management Symposium*, pp. 415–434.

APPENDIX II

Pötzelsberger, E., Hasenauer, H., 2015. Forest–water dynamics within a mountainous catchment in Austria. Nat. Hazards. doi: 10.1007/s11069-015-1609-x

Erratum:

In Table 3 (Appendix) units and values of VPD_{open} and Ψ_{open} and VPD_{close} and Ψ_{close} were confused.

Forest–water dynamics within a mountainous catchment in Austria

Elisabeth Pötzelsberger · Hubert Hasenauer

Received: 31 March 2014 / Accepted: 4 January 2015
© Springer Science+Business Media Dordrecht 2015

Abstract In this study, we assessed the role of forests in the local water budget within a 7.3 km² catchment that has measured river runoff and a long history of forest exploitation and disastrous flooding and debris flow events. Forests retain and absorb water from turning into runoff which is a possible trigger for catastrophic events. Forest water budgets (i.e. interception, transpiration, evaporation, sublimation, soil water storage and outflow) interact with ecosystem processes that are related to the carbon, nutrient and energy cycles and consequently affect forest growth rates. Therefore, we employed a biogeochemical–mechanistic ecosystem model, Biome-BGC, as a diagnostic tool to evaluate the dynamic relationships between key forest ecosystem characteristics and the water cycle. Our study was conducted in the Schmittental catchment with about 70 % forest coverage, situated in the Greywacke Zone of the Austrian Alps. Using stand and site information from 21 Norway spruce stands from the region and 29 years of total catchment runoff data for model validation, we demonstrated that the process-based ecosystem model mimics the interaction of forest growth and the water budget realistically. The weekly catchment runoff calculations based on Biome-BGC grid simulations compared well with observed runoff data. The analysis of the forest–water dynamics/relations showed that the water budget is affected by the size of the canopy and the physiological canopy behaviour in response to daily weather. The results suggested that for fully stocked stands and with a standing volume of >250 m³ ha⁻¹, forest water outflow was minimised.

Keywords Norway spruce · Ecosystem modelling · Water budget · Catchment runoff

E. Pötzelsberger (✉) · H. Hasenauer
Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna, Peter-Jordan-Str.
82, 1190 Vienna, Austria
e-mail: elisabeth.poetzelsberger@boku.ac.at

1 Introduction

Forests in mountainous areas are vital in providing a variety of ecosystem services (Sonnier 1991; Hamilton 1992) such as protection of human infrastructure by aiding in the avoidance or reduction in natural hazards such as flooding, debris flows or landslides (Brang et al. 2001; Berger and Rey 2004; Wehrli et al. 2007). Depending on the local situation, the protection function, as specifically defined in the Austrian Forest Act 1975 (amended 2002), is often more important than the production function since settlements and infrastructure must be protected to safeguard human life and livelihoods (Olschewski et al. 2012).

A major forest ecosystem service of mountainous forests is the prevention of high water runoff rates which are strongly regulated by the forest cover present within a given catchment (Markart et al. 2006). A surplus of soil water availability may result in high risks of soil erosion, shallow landslides, debris flows and flooding (Sidle et al. 1985). One of the fundamental roles of forests in the protection against excessive runoff is reduction in the runoff peaks. Forests regulate the water budget by intercepting and transpiring a large proportion of water (Engler 1919; Pallardy 2008), increasing the soil water holding capacity by encouraging the formation of a thick humus layer (Badoux et al. 2006; Uddling et al. 2008) and creating soil pores resulting from root growth that increase the infiltration capacity and thus the drainage of surface water into deeper soil layers (Aigner 1991; Lange et al. 2010).

In this study, we dealt with the forest–water dynamics/relations that describe the dynamic relationships between forest growth and the water balance (i.e. rainfall interception, water transpiration, evaporation, snow sublimation, soil water storage and out-flow). These dynamics are regulated by daily and gradually changing environmental growing conditions (weather, atmospheric CO₂ and nitrogen deposition). Hydrological models are commonly employed in catchment runoff studies to understand rainfall–runoff relations by tracking the movement of water in the soil as well as the catchment stream network in a high temporal and spatial resolution. In a review of hydrological models for forest management and climate change applications, Beckers et al. (2009) concluded that forest growth is largely missing in the surveyed models and that there is a need for forest leaf area and stomatal conductance information varying in space and time as well as for a better understanding of the impact of changing growing conditions.

One option to integrate these processes is the application of biogeochemical–mechanistic (BGC) ecosystem models. BGC-models are explicitly designed to predict forest productivity derived from the interaction of carbon, water, nutrient and energy cycles. Simulations of forest productivity incorporate environmental conditions, vegetation types, disturbance history and stand development stages (Hasenauer et al. 2000; Thornton et al. 2002). BGC-models incorporate responses to forest management (Merganičová et al. 2005; Petritsch et al. 2007) and potential changes in growing conditions such as climate change as well as increasing nitrogen deposition rates (Eastaugh et al. 2011; Warren et al. 2011). Thus, BGC-models have the potential to add crucial data on forest–water dynamics to hydrological model calculations of catchment water balances and improve the representation of the forest protection function.

The purpose of this paper was to link forest site and stand data as well as long-term catchment runoff measurements with the Biome-BGC model (Thornton et al. 2002; Pietsch et al. 2005). We assessed the forest–water dynamics and modelled the water budget dynamics and the catchment runoff within the Schmittental valley. The Schmittental valley is one of the few ‘small hydrological catchments (<25 km²)’ in the Alps with long-term

high-resolution data on precipitation and runoff (Geitner et al. 2009). Our specific research questions sought to:

- Validate a biogeochemical–mechanistic ecosystem model (Biome-BGC) to a mountainous catchment
- Identify key dynamic forest–water relations from Biome-BGC simulations that are relevant for the forest stand water budget and specifically for the outflow formation in managed forests
- Simulate catchment runoff in the Schmittental valley based on the analysed forest–water dynamics and compare simulated runoff with catchment runoff observations

2 Materials and methods

2.1 Study area

The study area is the Schmittental valley near Zell am See in the Austrian province of Salzburg. It belongs to the eco-region ‘2.2 Northern Transitional Alps-Eastern Part’ (Kilian et al. 1994) where the predominate tree species is Norway spruce (*Picea abies* (L.) Karst). The bowl-shaped Schmittental valley is approximately 10 km² with elevation ranging from 1,965 m (peak Schmittenhöhe) in the west to 750 m (lake Zeller See) in the east (Fig. 1). The average annual precipitation in the study area is about 1,500 mm, and the average temperature is 4.6 °C for the period 1981–2009. The watershed is drained by the river

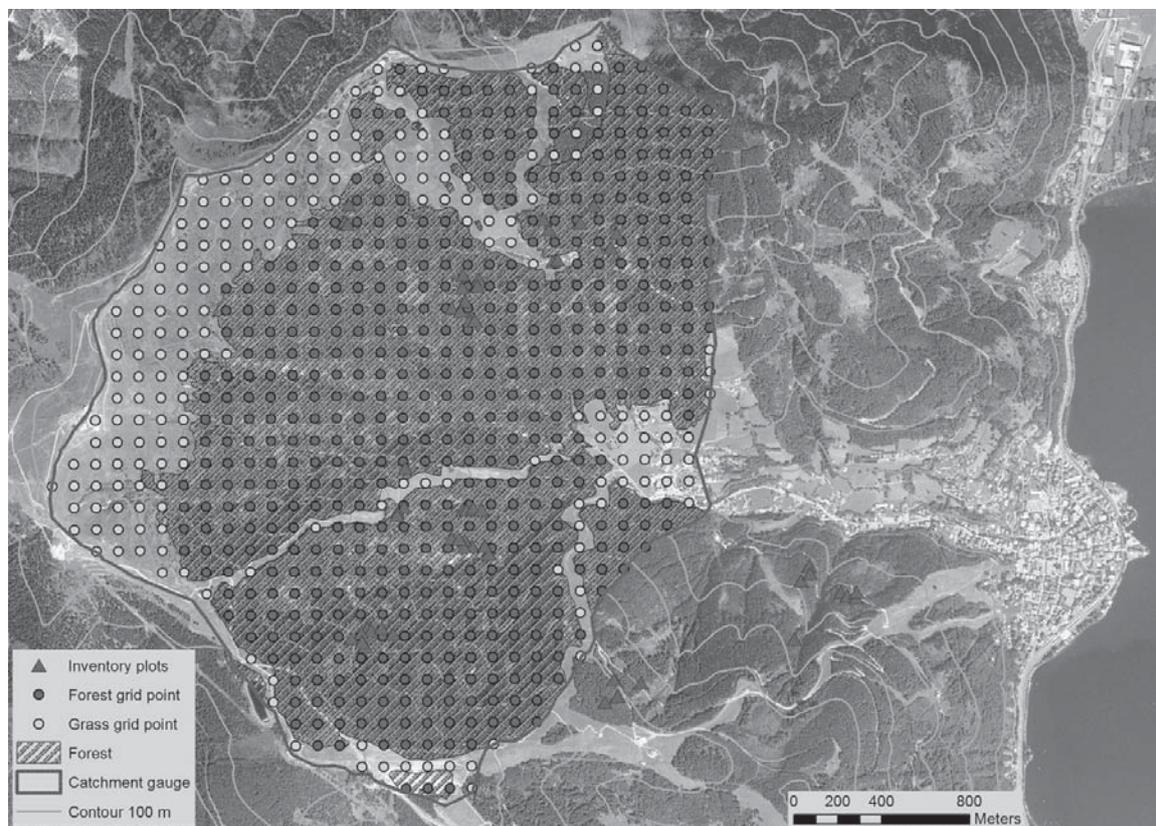


Fig. 1 Schmittental valley with the catchment of the river Schmittenbach gauge, forest cover, observed forest plots and grid simulation points

Schmittenbach. The city of Zell am See with close to 10,000 inhabitants is situated on and around the alluvial cone of the river Schmittenbach. The valley also contains a ski resort with currently 77 km of ski runs (Schmittenhöhebahn 2014). The watershed is located in the Greywacke Zone and mostly consists of 'Wildschönauer Shale', also called 'Pinzgauer Phyllite'. Shale predominates with interstratified thin-layered, fine-grained sandstone and clay, with a low proportion of Quartz. The soils contain large quantities of fine debris from easy weathering and consequently are compacted, limiting infiltration rates (Hagen 2003).

Forests are managed as age class forests. The forest area has experienced dramatic changes during the last 300 years. Overexploitation of the forest for logging, pasture and grazing, including loss of forest cover along the high ridges, had reduced forest coverage (Thoma 1900; Hagen 2003). In the 1880s, the area mapped as forest was 600 ha (57 %), however, at least 10 % of that area were barely stocked (Thoma 1900). More than 30 ha of bare soil were exposed, especially along the creeks. As a result, disastrous floods and landslides related to poor forest cover have repeatedly hit the area in recent centuries (Hagen 2003). At the end of the nineteenth century, reforestation programs were initiated and this increased forest coverage up to 77 % by 1987 (WLV 1996). Today, the catchment of our runoff analysis exhibits 71 % forest cover (520 ha), 28 % grassland (200 ha) where half of the grassland is in use as ski slopes (100 ha), and 1 % of the area are settlements and roads (10 ha) (see Fig. 1).

2.2 Forest data

We obtained tree, stand and site (elevation, slope and aspect) information from 21 Norway spruce (*Picea abies* (L.) Karst) stands covering the range in age classes, site conditions and productivity levels. For each selected forest stand, sized a few hectares, four sample plots were randomly selected to determine the standing timber volume using angle-count sampling (Bitterlich 1948). For each tree selected within a given sample plot, the diameter at breast height (DBH) and the tree height were recorded. Dominant tree height was derived according to Pollanschütz (1971) by calculating the mean height of the three thickest trees on each sample plot.

The tree representing the 50th percentile in the DBH distribution on each sample plot was selected to drill an increment core at breast height. For calculating the tree age, 15 years were added to the increment core to address the time needed to reach breast height. Stand density was defined according to Reineke (1933; SDI, stand density index) and may be considered as a site quality and age independent species-specific density index, defined by the number of trees of an equally dense stand with a quadratic mean diameter of 25 cm. Site index (dominant height at the age of 100 years) was determined using age and dominant height of the yield tables for 'Fichte Hochgebirge' ('Spruce high mountains') of Marschall (1975). Summary statistics of the forest stand data available for this study are given in Table 1.

2.3 River runoff data

Runoff data from the river Schmittenbach were collected by the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW) since 1978. For this study, we obtained daily runoff data for the period 1981–2009. The gauge at the river is located about 2 km upstream from the lake Zell am See (Fig. 1) at an elevation of 905 m. The gauged catchment size is 7.3 km². In a trapezoidal-shaped flume with a length of 10 m and a slope of 1 %, a strip chart recorder permanently recorded the water level through a float until

Table 1 Site and stand parameters, i.e. elevation (m a.s.l.), slope (°), aspect (°), stand age (years), dominant height (m), quadratic mean diameter (cm), stand density index SDI, volume measured (m³ ha⁻¹) and site index SI, of the 21 observed forest stands; minimum, maximum, median and mean are given

Parameter	Minimum	Maximum	Median	Mean
Elevation (m a.s.l.)	944	1,672	1,360	1,325
Slope (°)	25	45	35	34
Aspect (°)	34	300	118	–
Stand age (years)	31	142	79	75
Dominant height (m)	14	37	27	26
Quadratic mean diameter (cm)	13	50	27	27
Stand density index SDI	1,018	1,610	1,193	1,239
Volume (m ³ ha ⁻¹)	288	996	623	651
Site Index SI	23.5	36.6	29.8	30.2

2002. In addition, an electronic data logger collected 15-min interval values averaged from 5-min water level measurements since 1991. Since 2002, an ultrasonic gauge has recorded 5-min water levels. A parameterised rating curve was used to calculate runoff (Hagen 2003). For the study period, 874 days (8 % of the days) had missing or flawed runoff data unsuitable for further analysis due to measurement device breakdowns, ice, debris or mud. Days with high runoff values of more than 800,000 m³ d⁻¹, which represent according to Hagen (2003) a 100-year runoff event, were excluded from our analysis.

Recorded annual water runoff for years without missing days was 8.0 Million m³ year⁻¹ on average and ranged from 5.9 to 11.0 Million m³ year⁻¹. A linear trend over these full years ($n = 15$) revealed an increase in annual runoff ($p = 0.005$) with a slope parameter of 0.13 Million m³ year⁻¹. Monthly runoff was highest in May (1.4 Million m³ year⁻¹ on average), at times of snowmelt, and lowest in February. For May, the share of the highest daily runoff in the total monthly runoff was low, at about 5 %, indicating a continuous and long lasting snowmelt in a generally snow-rich area (Hagen 2003). The runoff coefficient, calculated from river runoff and total catchment precipitation (interpolated from DAYMET, see next section) for the hydrological years (September of the previous year to August), was 0.74 on average, with a standard deviation of 0.13. The high runoff coefficient is primarily attributed to dense soils but also to ski slopes that increase surface runoff (Hagen 2003).

2.4 Climate data

Daily weather data are important model drivers for assessing the water balance. More than 400 Austrian climate stations from the Austrian Central Institute for Meteorology and Geodynamics (ZAMG) were obtained to generate 50 years (1960–2009) of daily data for points within the catchment using DAYMET (Thornton et al. 1997). DAYMET is a climate interpolation and simulation tool originally developed for North America (Thornton et al. 1997) and adapted and validated for Austria (Thornton et al. 2000; Hasenauer et al. 2003). With DAYMET, we calculated daily minimum and maximum temperature (T_{\min} , T_{\max}), precipitation (Prcp), solar radiation (Srad) and vapour pressure deficit (VPD) at each simulation point in the catchment. Altitude, geographic coordinates and the east and west horizon angles were used as input to DAYMET. Details on the interpolation algorithms are given in Petritsch and Hasenauer (2014).

2.5 The ecosystem model

For our study, we used the daily time step biogeochemical–mechanistic ecosystem model Biome-BGC version 4.1.1 (Thornton et al. 2002; White et al. 2000). Biome-BGC is a process model that can be used in studying forest ecosystem dynamics to address flux dynamics and states, or cycles of energy, water, carbon and nitrogen on a daily basis. We incorporated extensions on species-specific parameters (Pietsch et al. 2005; Merganičová et al. 2012) and self-initialisation (Pietsch and Hasenauer 2006).

The general simulation procedure consists of the spin-up or self-initialisation with the dynamic mortality routine for obtaining carbon and nitrogen pool sizes at an equilibrium (Pietsch and Hasenauer 2006). The spin-up is followed by the historic land use as a sequence of clear cuts and plantings (rotations) and thinnings to consider management-related impacts on productivity (degradation) (Pietsch and Hasenauer 2002).

Key input variables for the model include daily meteorological data, ecosystem type, physical properties of soil, atmospheric CO₂ concentration, nitrogen deposition, disturbance history and forest management. The main simulated carbon and nitrogen cycle processes are stomatal carbon uptake, photosynthetic assimilation, growth and maintenance respiration, carbon and associated nitrogen allocation to leaves, roots and the stem, leaf onset, litter fall, mineralisation, soil carbon and nitrogen transformation and nitrogen volatilisation and leaching.

In the model, the forest canopy consists of sun and shade leaves expressed as leaf area index (LAI, m² leaves per m² soil surface) which controls the radiation absorption, photosynthesis, litter production, water interception and transpiration. Water enters the model through daily total precipitation, either as rain ($T_{\text{avg}} > 0$) or as snow ($T_{\text{avg}} \leq 0$). Rainfall is partially intercepted by the canopy (interception I) depending on LAI, an interception coefficient k , and precipitation intensity according to the following simple equation, $I = k \cdot \text{LAI} \cdot \text{Prcp}$ (Thornton 1998). k is given in the Appendix; Table 3. The remaining water is directly routed to the soil water pool. Partial evaporation of intercepted water occurs on the same day as the rainfall. Water not evaporated on the same day is added to the soil water pool. Snowmelt occurs on days with positive air temperature. On freezing days, water sublimates from the snowpack using solar energy inputs. Based on empirical pedotransfer functions (Clapp and Hornberger 1978; Cosby et al. 1984; Saxton et al. 1986) (see Appendix; Table 4), the soil water holding capacity at saturation is derived from soil depth and texture. Water above saturation is lost immediately as outflow as an equivalent to overland flow (Thornton 1998). Between saturation and field capacity (−0.015 MPa), water drains at a rate of 50 % per day. With this exponential decay that approaches field capacity, 12.5 % of the water between saturation and field capacity are left after 3 days. The remaining soil water is considered accessible for evaporation and transpiration. Evaporation is calculated with the Penman–Monteith equation and depends on air temperature, pressure, VPD, solar radiation, the transport resistance of water vapour and sensible heat and the days since the last rain event. Transpiration uses the Penman–Monteith equation and is regulated by stomatal conductance. Maximum stomatal conductance ($g_{s,\text{max}}$, Appendix; Table 3) is limited with multipliers [0,1] that depend species specifically on VPD, soil water potential (Ψ) and daily minimum temperature (T_{min}) and generally on intercepted solar radiation (Appendix; Table 5). Leaf-level conductance uses an electric circuit analogy where stomatal conductance and cuticular conductance are in parallel and boundary conductance is in series (Appendix; Table 5, Eq. 7). For further details, we refer to Thornton (1998), White et al. (2000), Thornton et al. (2002) and Pietsch and Hasenauer (2006).

2.6 Modelling procedure

For the simulations, we used the ecophysiological parameter set for Norway spruce (Pietsch et al. 2005) and the standard C3-grass parameter set of White et al. (2000). Within the catchment area, Biome-BGC simulations on a 100 m × 100 m grid (722 grid points) were performed. The modelling procedure started with the model self-initialisation run using Norway spruce forest parameterisation for all 722 grid points assuming full forest coverage. According to the current land cover distribution, we separated the grid points into forested land (521 grid points) and non-forested land, primarily grassland (201 grid points; Fig. 1). For management scheduling purposes, the 521 forest grid points were randomly assigned a forest stand age between 1 and 120 years representing the age range of forest stands present within the study region. Historic land use impacts were addressed by two rotations (of 120 years), separated by clear cut and planting, prior to the planting of the actual stand. Thinning regimes according to Petritsch (2008) were applied. The 201 grid points on non-forested land were simulated as grassland covering a 400-year period, following the spin-up with Norway spruce.

Next, we applied the same procedure for the 21 observed forest stands, with the exception that the stand age was known instead of randomly assigned for scheduling the clear cut and planting and thinning interventions.

Daily weather data for the years 1960–2009, used as model drivers, were interpolated to the simulation points with DAYMET. For the spin-up and the years before 1960, we used 50-year climate data repeatedly and randomly (full years). Atmospheric CO₂ concentration was kept constant at the preindustrial CO₂ concentration of 280 ppm (Enting et al. 1994) for the spin-up and permitted an increase starting from the beginning of the industrial revolution to current levels, as described by the IPCC's IS92a curve for CO₂ (IPCC 1992). A preindustrial nitrogen deposition of 0.005 kg N m⁻² year⁻¹ was assumed, similar to Pietsch et al. (2005). Current nitrogen deposition rates for Austria were taken from an annual nitrogen deposition map for the reference year 1996 based on two studies conducted by the Austrian Federal Environment Agency (Schneider 1998; Placer and Schneider 2001) and compiled by Eastaugh et al. (2011). Between preindustrial and current levels, annual deposition was assumed to experience the same relative increase as atmospheric CO₂. Nitrogen fixation was set to a fixed level of 0.003 kg N m⁻² year⁻¹. Soil texture and effective soil depth were interpolated from the measurements of the Austrian National Forest Soil Survey (Petritsch and Hasenauer 2007).

2.7 Catchment runoff

For catchment runoff estimates, we used the simulated point outflow (dm³ m⁻²) representing plot outflow from Biome-BGC forests and grassland simulations based on the 100 m × 100 m grid (Fig. 1). To account for a delay in river runoff formation and some intermediate storage of water deeper down in the rock, we developed a simple temporal weight factor array for simulated plot water outflow based on a local hydrological transfer function, following a decreasing exponential function, (Eq. 1):

$$N(t) = N_{\min} - \left(N_{\min} - N_0 \cdot \frac{A_m}{A} \right) e^{\lambda t} \quad (1)$$

where $N(t)$ is the proportion of simulated plot outflow that is added to catchment runoff on day t after the simulation of the plot outflow, N_0 is the proportion of simulated plot outflow that is added to catchment runoff on the day of the simulation, N_{\min} is the outflow

proportion that is asymptotically approached after t days, A_m is the mean elevation in the catchment, A is the elevation of the simulation point, λ is a shape parameter between 0 and 1 and t is the day after the outflow simulation $[0, t]$. Parameter values used in this study were $N_0 = 0.1$, $N_{\min} = 0.005$, $A_m = 1,450$ and $\lambda = 0.2$. We parameterised N_0 , N_{\min} and λ to yield optimised agreement between average weekly catchment runoff calculations and measurements. Using the temporal weighting factor array, simulated daily plot water outflow was distributed over a certain number of days. The length and values of the temporal weighting factor array depended on elevation, as in our bowl-shaped catchment elevation could be used as a proxy for the distance to the river runoff gauge. The length was determined by calculating the cumulative sum of the temporal weights until the sum was 1. After simulated daily plot outflow had been distributed over a specific time period as prescribed by the weighting factor array, all the plot outflow assigned to a certain day was added up to yield catchment runoff.

3 Analysis and results

3.1 Model validation

For each of the 21 model validation stands, we applied Biome-BGC using the ecophysiological parameterisation for *Picea abies* (Pietsch et al. 2005). Predicted stem carbon was converted into stand volume using the biomass expansion factor (Pietsch et al. 2005) to compare predicted versus observed stand volume. Main statistical results of the model validation are summarised in Table 2. Mean predicted and observed volume were 615 and 651 $\text{m}^3 \text{ha}^{-1}$, respectively. Standard deviation of the differences between predicted and observed values ranged between 88 $\text{m}^3 \text{ha}^{-1}$ and 14 % of the observed mean volume (Table 2). The paired Student's t test exhibited no significant difference between predicted and observed volume ($\Delta = 37 \text{ m}^3 \text{ha}^{-1}$, $t = 1.91 < t_{\alpha} = 0.025, N = 21 = 2.09$). One approach to determine the limits and range of error in predictions is to calculate the confidence and prediction intervals. The confidence interval CI for the mean of the differences D (predicted–observed) was used to evaluate discrepancies between the expected difference and the estimator \bar{D} . The prediction interval PI gives the range of the differences (D_i) between predictions and observations (Reynolds 1984). With a probability of 95 %, we were confident that for the mean, the bias was between -77 and $3 \text{ m}^3 \text{ha}^{-1}$ and thus not significantly different from zero (unbiased). With a probability of 95 %, we could be confident that a single future difference in the volume predictions of Norway spruce would be between -225 and $152 \text{ m}^3 \text{ha}^{-1}$ (Table 2).

Table 2 Results of the error analysis for the volume per hectare of the validation plots

$\overline{\text{obs}}$	\bar{D}_i	SD	t	CI	PI
651	-37 (-6%)	88 (14 %)	1.91	-77 to $+3$ (-12 to $+1 \%$)	-225 to $+152$ (-35 to $+23 \%$)

Values are given in $\text{m}^3 \text{ha}^{-1}$; values in parentheses are percent of the observed volume

$\overline{\text{obs}}$ is the mean of observations, \bar{D}_i the mean of the differences between predicted and observed values, SD the standard deviation of the differences and t the value from the paired t statistics. CI and PI are the confidence and prediction intervals calculated as $\text{CI} = \bar{D} \pm \frac{\text{SD}}{\sqrt{n}} \cdot t_{1-\alpha/2(n-1)}$ and $\text{PI} = \bar{D}_i \pm \sqrt{1 + \frac{1}{n}} \cdot \text{SD} \cdot t_{1-\alpha/2(n-1)}$, respectively, with n as the sample size, t as the $1 - \alpha/2$ quantile of the t -distribution with $n - 1$ degrees of freedom and the error $\alpha = 0.05$ (Reynolds 1984)

Volume results were tested for consistency by plotting standardised residuals against the main stand and site characteristics: (I) elevation, (II) slope, (III) aspect, (IV) stand age, (V) dominant height, (VI) quadratic mean diameter, (VII) SDI and (VIII) stand volume (Fig. 2). No bias was detected ($\alpha = 0.05$), suggesting that Biome-BGC properly captures the flux dynamics including the water cycle for the forests within our catchment area.

3.2 Forest–water dynamics

Forest–water dynamics were analysed based on 100×100 m gridded Biome-BGC simulations within the catchment. The analysis included the simulation results of all 521 forest grid points and included their forest stand growth over the previous two 120-year rotation

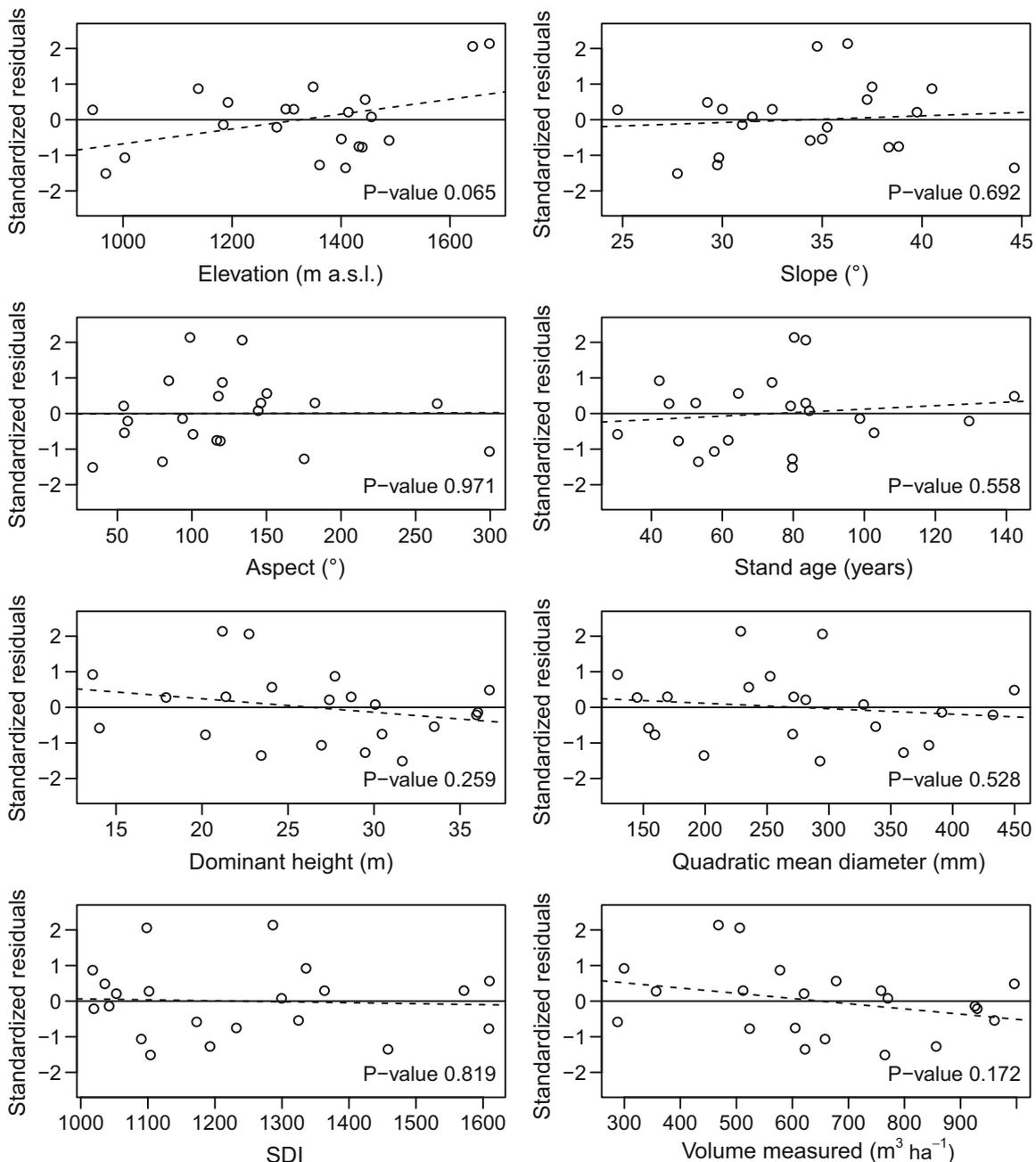


Fig. 2 Trend analysis of standardised volume residuals versus site and stand parameters and variables, i.e. elevation (m a.s.l.), slope ($^{\circ}$), aspect ($^{\circ}$), stand age (years), dominant height (m), quadratic mean diameter (mm), stand density index SDI and volume measured ($\text{m}^3 \text{ha}^{-1}$)

periods and the growth history of the simulated present-day forest stands. Forest water retention and consumption was simulated by the model using variables including (1) canopy evaporation; (2) soil evaporation; (3) snow sublimation; and (4) transpiration—summarised as evapotranspiration (ET). These processes affect and/or depend on forest growth, as growth is strongly linked to size and physiology of the forest canopy, and on the soil water status. In the model, the stand canopy is represented as leaf area index (LAI), the decisive plant compartment for productivity (gas exchange of CO₂ used in photosynthesis) and water cycle processes (interception, transpiration, ground shade influencing evaporation and snowmelt; Running 1992).

We started our analysis of the forest–water dynamics using a key soil parameter, soil water potential (Psi) that regulates transpiration through stomatal conductance regulation and soil water storage and outflow (see Sect. 2.5.). Weather, forest growth and soil drainage regulate daily changes in Psi. The behaviour of Psi over the course of two exemplary years (1981 and 2007) showed to differ for different LAI classes (LAI 0–1, 1–2, ..., 7–8; Fig. 3), averaged from all 521 forest grid point simulations. Thus, we next explored the influence of the forest canopy (LAI) on the water cycle of a forest stand. Figure 4 shows the estimated annual transpiration (Tr), evaporation (E) and water use efficiency (WUE, in g C m⁻² mm⁻¹ H₂O, calculated as NPP/ET; Pallardy 2008) versus LAI for the 521 forest grid points.

As for practical forest management issues, stand volume and stand density index (SDI) are key stand measures; we next assessed the correlations between LAI and standing timber volume, SDI and elevation. Figure 5 presents simulated LAI versus the observed timber volume and the observed SDI for the 21 observed forest stands, and simulated LAI versus the predicted timber volume (in 100 m³ ha⁻¹ classes), and the elevation (in 100 m classes) for all 521 forest grid points.

The most relevant water budget component in mountainous areas is the water outflow due to its contribution to soil erosion, floods and debris flows. A linear regression analysis showed no significant trend of simulated annual outflow versus measured timber volume or SDI ($p = 0.777$, $p = 0.554$). Evidently, LAI had a strong impact on annual plot outflow (Fig. 6, left), while timber volume did not, except for timber volumes <250 m³ ha⁻¹ (Fig. 6, right). The relative contributions of the five output components of the annual water budget (1) canopy evaporation of intercepted water, (2) soil evaporation, (3) snow sublimation, (4) transpiration and (5) outflow by LAI and volume classes are given in Fig. 7.

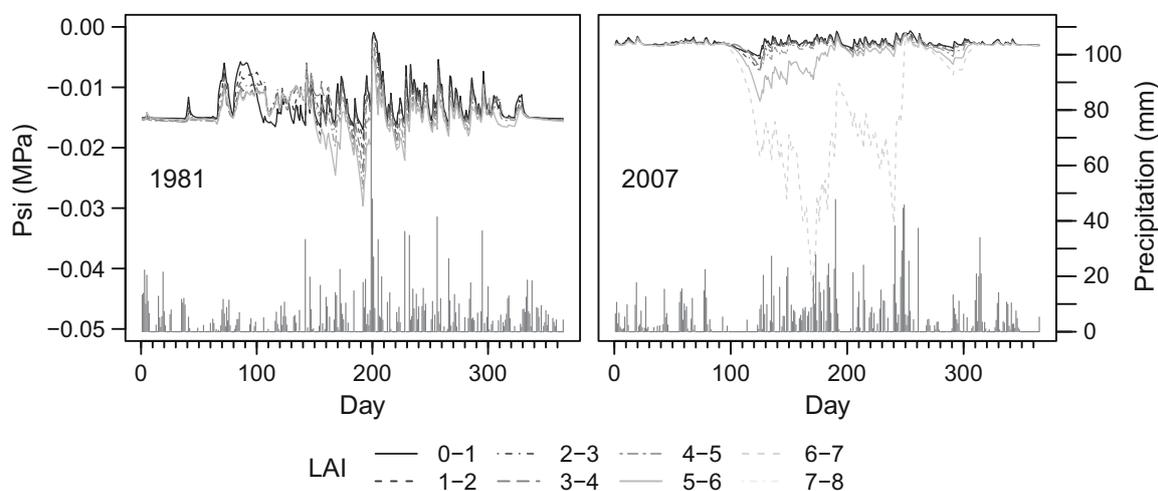
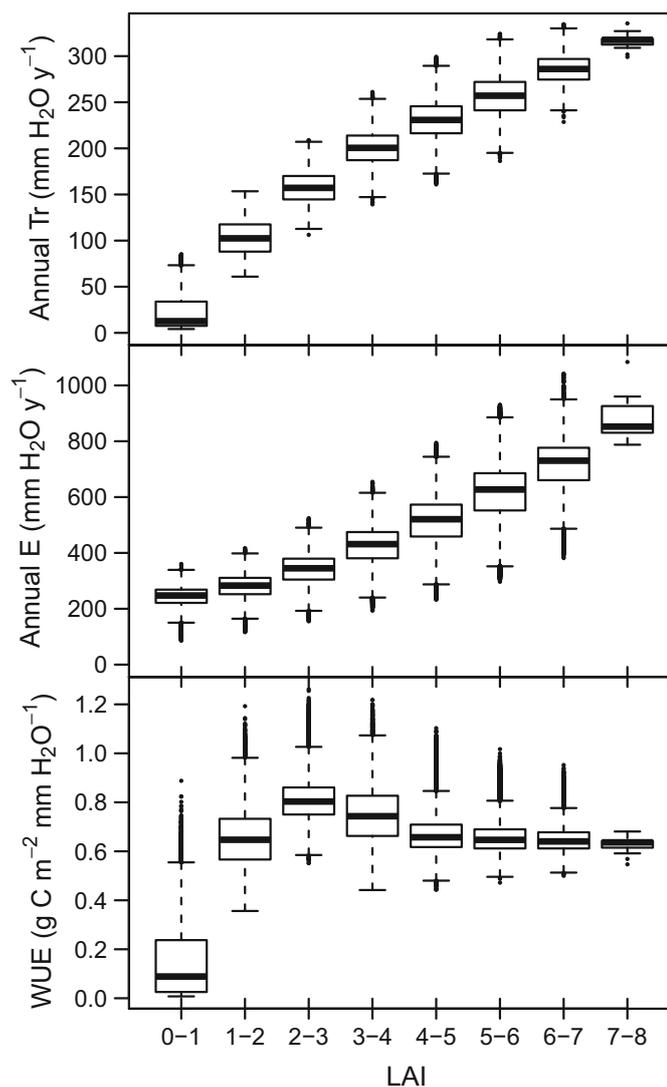


Fig. 3 Soil water potential (Psi) changes over the course of two exemplary years (1981 and 2007). Daily Psi values of all 521 forest grid points are averaged over leaf area index (LAI) classes

Fig. 4 Annual transpiration (Tr , $\text{mm H}_2\text{O year}^{-1}$) (*top*), evaporation (E , $\text{mm H}_2\text{O year}^{-1}$) (*middle*) and water use efficiency (WUE , NPP/ET , $\text{g C m}^{-2} \text{mm}^{-1} \text{H}_2\text{O}$) (*bottom*) versus leaf area index (LAI) classes for the 521 Norway spruce grid points for the past two rotations and the present-day stand. Data are presented as *box and whiskers plots*, where the end of the *line* is at the last data point that is inside the maximum distance from the *box* that is the 1.5-fold length of the *box*



3.3 Catchment runoff

Based on the above-mentioned calculations of forest–water dynamics, we calculated catchment runoff using 100×100 m gridded Biome-BGC simulations for the whole catchment and the hydrological transfer function. Total catchment runoff was governed by the water balances at the different forest and grassland sites. Daily Schmittentbach river runoff data for comparison were available for the period 1981–2009. For comparability, the days of missing measurements had been removed from the simulation results. Recorded annual water runoff for years without missing days ranged from 5.9 to 11.0 Million $\text{m}^3 \text{year}^{-1}$ whereas simulation results for the full record years ranged from 4.8 to 7.3 Million $\text{m}^3 \text{year}^{-1}$. We present simulated and observed annual runoff relative to the corresponding mean annual runoff (due to some uncertainties in absolute values, see next section) for the period 1981–2009 (Fig. 8). We also show full catchment precipitation and water runoff predictions versus the observed runoff (Fig. 9).

4 Discussion and conclusion

The biogeochemical–mechanistic ecosystem model Biome-BGC provided consistent and unbiased volume estimates (Fig. 2; Table 2). The corresponding residuals showed no trend

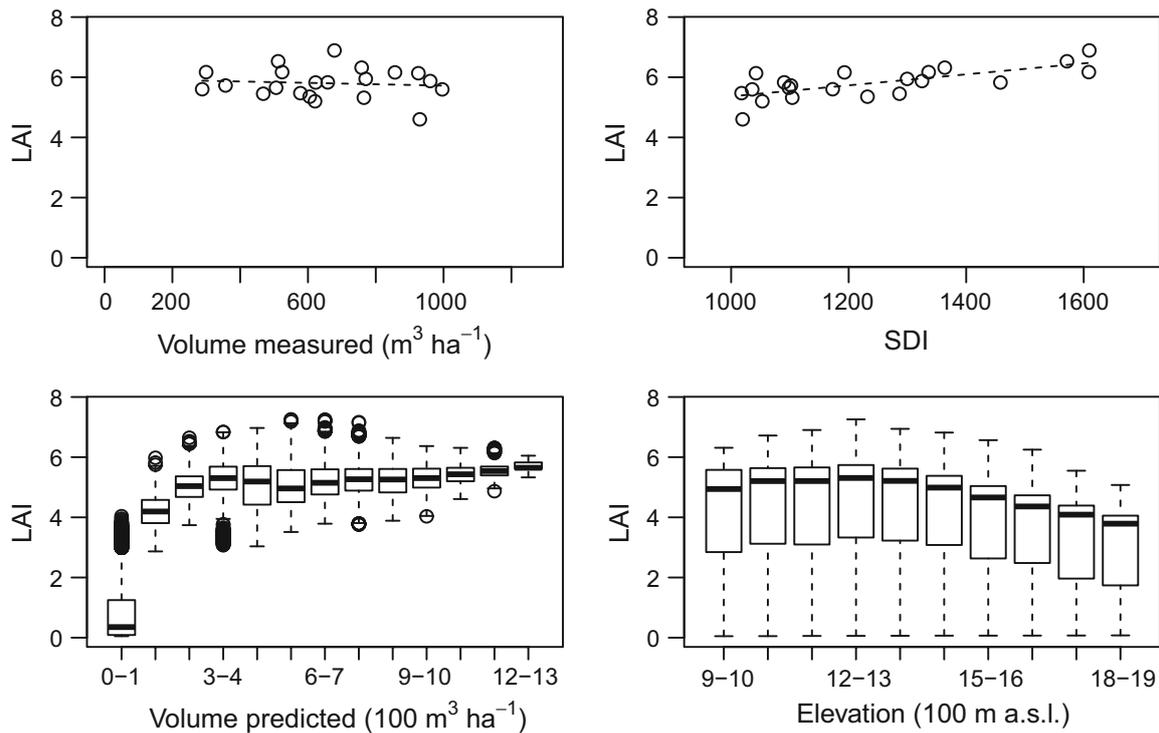


Fig. 5 Leaf area index (LAI) versus measured timber volume (*top left*) and stand density index (SDI) for the 21 Norway spruce observation stands (*top right*) and LAI versus predicted timber volume classes ($100 \text{ m}^3 \text{ ha}^{-1}$) (*bottom left*) and versus elevation classes (100 m a.s.l.) (*bottom right*) for the 521 Norway spruce grid points for the past two rotations and the present-day stand. Data of LAI versus volume and elevation are presented as *box and whiskers plots*, where the end of the *line* is at the last data point that is inside the maximum distance from the box that is the 1.5-fold length of the box

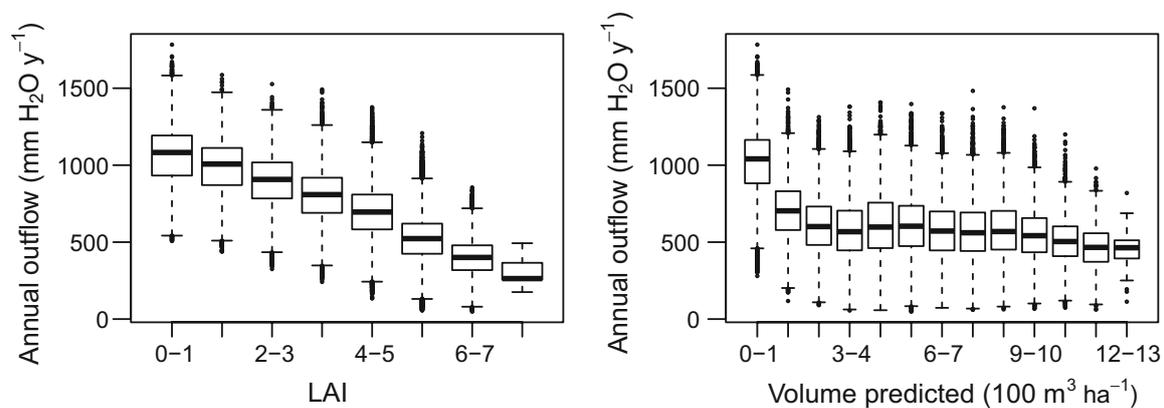


Fig. 6 Annual outflow versus leaf area index (LAI) classes (*left*) and predicted timber volume classes ($100 \text{ m}^3 \text{ ha}^{-1}$) (*right*) for the 521 Norway spruce grid plots for the past two rotations and the present-day stand. Data are presented as *box and whiskers plots*, where the end of the *line* is at the last data point that is inside the maximum distance from the box that is the 1.5-fold length of the box

versus site (elevation, slope and aspect) and stand characteristics (stand age, dominant tree height, quadratic mean diameter, stand density and volume), suggesting that the underlying ecosystem fluxes were unbiased.

Soil water potential (Psi) regulates soil water storage but also is an important regulator of stomatal gas exchange (CO_2 goes in and water vapour out) which influences tree growth rates and ultimately runoff from the forest stand. The pattern of Psi varied with the LAI of

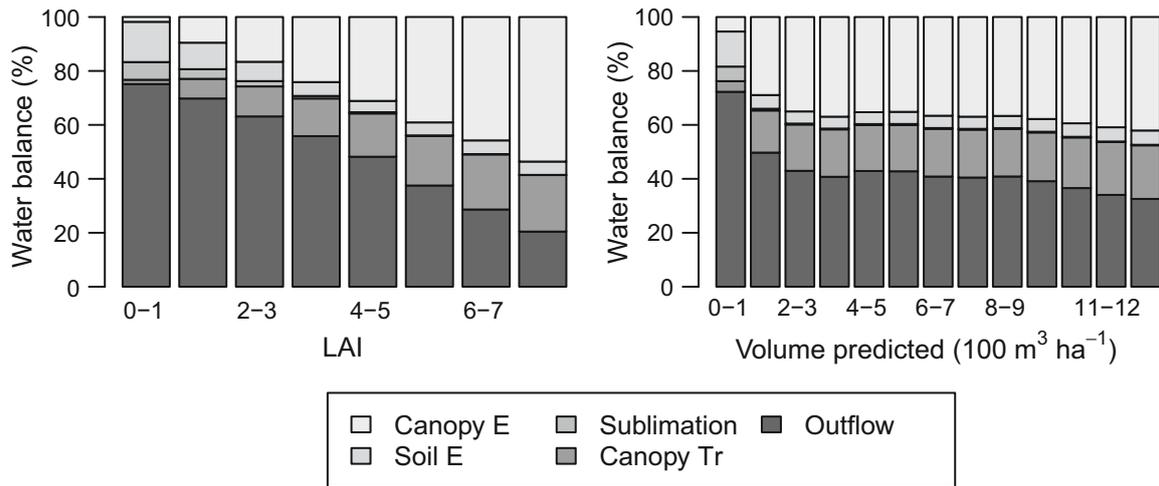


Fig. 7 Water output components constituted by canopy evaporation (E), soil evaporation, sublimation from the snow cover, canopy transpiration (Tr) and plot outflow presented as relative values (%) versus leaf area index (LAI) classes (*left*) and predicted timber volume classes ($100 \text{ m}^3 \text{ ha}^{-1}$) (*right*), averaged from the 521 Norway spruce grid points for the past two rotations and the present-day stand

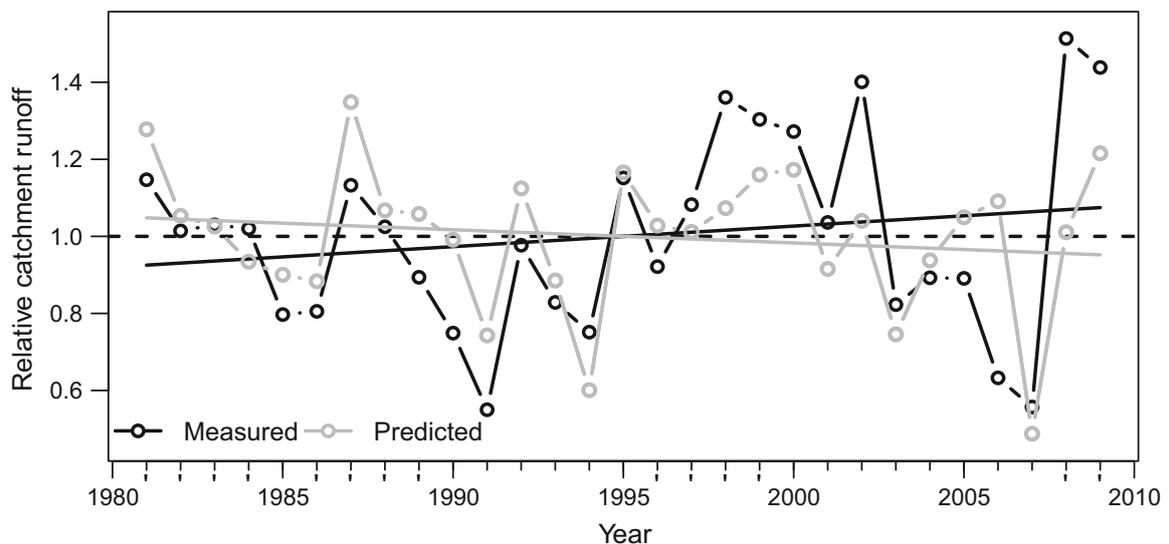


Fig. 8 Annual catchment runoff relative to the mean annual runoff from gauged Schmittental valley catchment (*black*) and calculations from Biome-BGC grid simulations (*grey*). Days with missing or erroneous measurements are removed, also from the simulations. Years with a full record are marked with a *comma* at the year tick

the forest stand. In particular, during the spring snowmelt, the stands with a higher LAI showed an extended period of high soil water potential (Fig. 3, left), while during the growing season, Psi dropped to the lowest values in stands with the highest LAI. In particular, the effect during the growing season depends, amongst others, on physiology regulated processes (transpiration, LAI development influencing interception and shading) what underlines the importance of dynamic forest–water relations in water balance assessments. Annual transpiration (Tr) and annual evaporation (E) increased with increasing LAI (Fig. 4). However, the increase in annual Tr gets smaller with increasing LAI because the ratio of sun and shade canopy becomes dominated by shade leaves, and these shade leaves have an increasingly limited stomatal conductance due to little available solar radiation. Evaporation, composed of soil E and canopy E, tends to increase more with

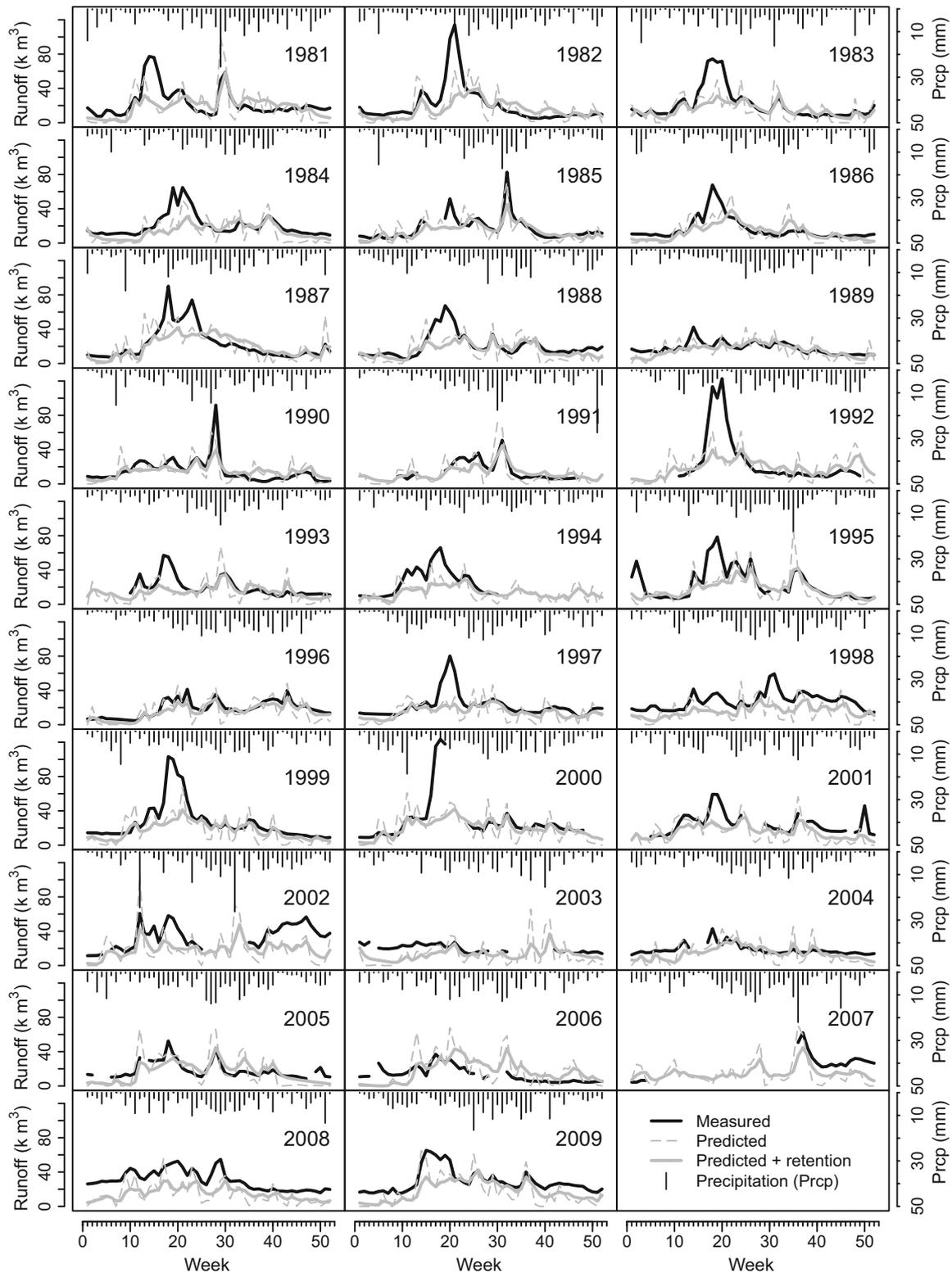


Fig. 9 Weekly Schmittental catchment precipitation and runoff for all measurement years; measured data from the runoff gauge at the river Schmittenbach (*black*), runoff data calculated from grid simulations with Biome-BGC (*grey, dashed*) and runoff calculated from the same simulations applying the hydrological transfer function (*grey*). Weeks with missing measurements have gaps in the *black* line

higher LAI, as soil E decreases less with higher LAI than canopy E increases with higher LAI (Fig. 7). The water use efficiency (WUE, NPP/ET), often used in ecophysiological studies to describe forest–water relations, increased with increasing LAI and peaked at LAI

values of 2–3. At an LAI of 4, a plateau state is reached with a WUE of about 20 % below the peak (Fig. 4). This means that young stands are very efficient in the stand water consumption contributing to higher outflow rates and that mature forest stands with an $\text{LAI} \geq 4$ have stabilised their water use efficiency and thus can contribute in a more uniform way to water consumption and thus reduced outflow rates.

Obtaining field LAI measurements requires either expensive technical equipment or time-consuming laboratory analysis (Gower et al. 1999). Therefore, we wanted to relate simulated LAI with stand and site parameters commonly determined by foresters (e.g. forest stand volume estimates). No trend in LAI simulations versus measured volume was evident within the observed volume range of 300–1,000 $\text{m}^3 \text{ha}^{-1}$ for the 21 observed forest stands (Fig. 5). With the simulation results of the 521 forest grid points, we could show that LAI only depended on the volume of young stands with little volume and reached a maximum at a volume of around 250 $\text{m}^3 \text{ha}^{-1}$ (Fig. 5). Thus, stand volume may only be used to derive forest–water relations for young stands with still little stocking volume ($\leq 250 \text{m}^3 \text{ha}^{-1}$). Elevation had a negative impact on LAI in mid- to high elevations (1,250–1,850 m), where the median LAI decreased from 5.3 to 3.8. A similar elevation trend was observed in other Alpine valleys (Bobeva 2003).

As suggested by the increase in E and Tr with LAI (Figs. 4, 7), the annual outflow decreased with LAI (Figs. 6, 7). Annual outflow versus timber volume showed that the outflow rates stabilised at a minimum stand volume of about 250 $\text{m}^3 \text{ha}^{-1}$ (Figs. 6, 7). Despite the positive linear trend of modelled LAI versus stand density ($p = 0.0003$) (Fig. 5), the simulated outflow was not correlated with the measured volume or the SDI of the observed forest stands (not shown). Apparently, the range of the observed volume was above the threshold level of 250 $\text{m}^3 \text{ha}^{-1}$ at which the outflow rates stabilised (Fig. 6), and also for the fully stocked Norway spruce stands with an observed SDI $\geq 1,000$ water outflow is minimal.

The catchment runoff simulations revealed consistent patterns between predicted and observed relative annual catchment runoff data (Fig. 8). Weekly simulated catchment runoff also compared well with observed catchment runoff data (Fig. 9), suggesting that the main water cycle fluxes are strongly connected to the carbon, nitrogen and energy cycle through forest growth. The runoff simulation results also supported the transfer function (Eq. 1), yielding consistent runoff flows. If we had not applied the transfer function which captures the time-lag effect of water transfer from the plot to the river runoff gauge, our results would have reflected increased weekly fluctuations of simulated versus observed runoff (Fig. 9). In particular during the growing season, we were able to track runoff patterns as governed by the dynamic interactions of weather, site and forest growth.

Results indicate uncertainty regarding the snowmelt peak runoff in spring and during extreme rainfall events in summer. Problematic are sealed surfaces (buildings, roads and parking lots, about 10 ha) and ski slopes (about 100 ha or 14 % of the catchment) with low infiltration rates (Hinterstoisser 1985) that had to be simulated as grasslands. An earlier irrigation experiment in the catchment, applying 100 mm h^{-1} , revealed a high surface runoff on ski slopes without grazing (18.4 % of precipitation), on ski slopes grazed with sheep (29.2 %), and very low surface runoff in forests (1.7 %; Schaffhauser 1982). Since surface runoff is a phenomenon hardly ever observed in forests (Engler 1919; Markart et al. 2006), surface runoff is not represented in the Biome-BGC model. Artificial snow, which has become important within Alpine regions to prolong the skiing season, was not considered in our catchment runoff calculations. Artificial snowmaking in the study region dates back to 1973, and in the late twentieth century, the average annual amount of water used was approximately 330,000 m^3 . Currently about 500,000 m^3 of water is used every

year to produce snow for the ski industry (H. Mayer, technical director of the Schmittenhöhebahn AG, personal communication). This amounts to 20–25 % of the average annual difference between the catchment runoff estimates and measurements and likely explains the frequent underestimation of peak snowmelt runoff in spring.

We conclude that a process-based ecosystem model is an important diagnostic tool for assessing important dynamic relationships between forests, environmental conditions and the water balance. Predicting changes to the water balance during the growth of a forest stand or as a response to forest management and changing environmental conditions can have important applications in the analysis of whole catchment water balances.

Acknowledgments Data on river Schmittenbach runoff for the years 1981–2005 were provided by the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW). 2003–2009 runoff data were provided by the Institute of Mountain Risk Engineering (IAN) of the University of Natural Resources and Life Sciences, Vienna. We are grateful to the ‘Landschaftliche Forstverwaltung Zell am See’ for their technical support and provision of historic forest inventory data. We thank Adam Moreno and Loretta Moreno for English editing. Last but not least we thank two anonymous reviewers for their thorough review and their valuable recommendations.

Appendix

Maximum stomatal conductance (g_{s_max} , Table 3) is limited with multipliers (m) [0,1] that depend species specifically on VPD, soil water potential (Ψ) and daily minimum temperature (T_{min}) and generally on intercepted solar radiation (Tables 4, 5, Eqs. 1, 2). For VPD below and Ψ and T_{min} above a certain threshold level ($_{open}$), the multiplier is 1, and thus, there is no conductance reduction; for VPD above and Ψ and T_{min} below another threshold level ($_{close}$), the multiplier is 0, and thus, there is complete stomatal closure. In between the two threshold levels, the conductance multiplier for VPD and Ψ changes linearly (Table 5, Eqs. 3–5). The solar radiation multiplier is calculated separately of the sun and the shade canopy. It considers the amount of radiation intercepted in the canopy ($PPFD_{pLAI}$, photosynthetically active photon flux density per projected LAI, $\mu\text{mol m}^{-2} \text{s}^{-1}$). This hyperbolic relationship needs the $PPFD_{50}$ value, giving the level of $PPFD_{pLAI}$ for which m_{Srad} is 0.5, defined as $75 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Thornton 1998). The intercepted radiation ($PPFD_{pLAI}$) differs between sun and shade leaves; thus, the conductance multiplier is calculated separately for sun and shade leaves (Table 5, Eq. 6). Consequently, also m_{total} (Table 5, Eq. 2) is calculated separately for sun and shade canopy. Final leaf-level conductance to transpired water (g_{trans}) uses an electric circuit analogy and is stomatal

Table 3 Selected ecophysiological constants relevant for the water and carbon budgets

Parameter (unit)	<i>Picea abies</i>	C3-grass
k ($\text{m}^2 \text{ LAI d}^{-1}$)	0.036	0.021
g_{s_max} (m s^{-1})	0.002	0.005
g_c (m s^{-1})	0.00006	0.0001
g_{bl} (m s^{-1})	0.09	0.04
VPD_{open} (MPa)	−0.5	−0.6
VPD_{close} (MPa)	−2.5	−2.3
Ψ_{open} (Pa)	500	930
Ψ_{close} (Pa)	1,500	4,100
T_{min_open} ($^{\circ}\text{C}$)	−2	−2
T_{min_close} ($^{\circ}\text{C}$)	−10	−10

The parameters for *Picea abies* are taken from Pietsch et al. (2005); for C3-grass, they are taken from White et al. (2000). Two obvious typos in the *Picea abies* parameters compared to the original publication were corrected ($g_{bl} = 0.09$ instead of 0.009 and $\Psi_{open} = 500$ instead of 50)

Table 4 Equations for soil water potential and volumetric water content in Biome-BGC (Thornton 1998)

Equations	Parameters	
$\Psi = \Psi_{\text{sat}} \left(\frac{\theta}{\theta_{\text{sat}}} \right)^b$	Ψ, Ψ_{sat}	Soil water potential, ~ at field capacity
$\Psi_{\text{sat}} = -9.8e - 5 \cdot \exp[(1.54 - 0.0095 \cdot P_{\text{sand}} + 0.0063 \cdot P_{\text{silt}}) \cdot \log(10)]$	$\Theta, \Theta_{\text{sat}}, \Theta_{\text{fc}}$	Volumetric water content, ~ at saturation, ~ field capacity
$\theta_{\text{sat}} = \frac{(50.5 - 0.142 \cdot P_{\text{sand}} - 0.037 \cdot P_{\text{clay}})}{100}$	B	Empirical shape parameter
$b = -3.10 - 0.157 \cdot P_{\text{clay}} + 0.003 \cdot P_{\text{sand}}$	$P_{\text{sand}}, P_{\text{silt}}, P_{\text{clay}}$	Percentage of sand, silt and clay ($\Sigma = 100$)
$\theta_{\text{fc}} = \theta_{\text{sat}} \left(\frac{-0.015}{\Psi_{\text{sat}}} \right)^{\frac{1}{b}}$	$W_{\text{fc}}, W_{\text{sat}}$	Soil water content at field capacity and at saturation
$W_{\text{fc}} = 1,000 \cdot d_{\text{soil}} \cdot \theta_{\text{fc}}$	d_{soil}	Effective soil depth (soil depth reduced by rock content)
$W_{\text{sat}} = 1,000 \cdot d_{\text{soil}} \cdot \theta_{\text{sat}}$		

Table 5 Equations for the regulation of stomatal conductance in Biome-BGC (Thornton 1998)

Eq. No.	Equations	Parameters	
1	$g_s = g_{s_max} \cdot m_{\text{total}}$	g_s, g_{s_max}	Stomatal conductance, maximum stomatal conductance
2	$m_{\text{total}} = m_{\text{VPD}} \cdot m_{\Psi} \cdot m_{T_{\text{min}}} \cdot m_{\text{Srad}}$	$m_{\text{total}}, m_{\text{VPD}}, m_{\Psi}, m_{T_{\text{min}}}, m_{\text{Srad}}$	Final stomatal conductance multiplier, multiplier for VPD, Ψ , Tmin and solar radiation
3	$m_{\text{VPD}} = \frac{(\text{VPD}_{\text{close}} - \text{VPD})}{(\text{VPD}_{\text{close}} - \text{VPD}_{\text{open}})}$	$\text{VPD}, \text{VPD}_{\text{open}}, \text{VPD}_{\text{close}}$	Vapour pressure deficit, VPD where stomata start to close and VPD where closure is complete
4	$m_{\Psi} = \frac{(\Psi_{\text{close}} - \Psi)}{(\Psi_{\text{close}} - \Psi_{\text{open}})}$	$\Psi, \Psi_{\text{open}}, \Psi_{\text{close}}$	Soil water potential, analogue to VPD
5	$m_{T_{\text{min}}} = 1.0 + \frac{(T_{\text{min}_{\text{open}}} - T_{\text{min}})}{(T_{\text{min}_{\text{close}}} - T_{\text{min}_{\text{open}}})}$	$T_{\text{min}}, T_{\text{min}_{\text{open}}}, T_{\text{min}_{\text{close}}}$	Daily minimum temperature, analogue to VPD
6	$m_{\text{Srad}} = \frac{\text{PPFD}_{\text{pLAI}}}{(\text{PPFD}_{50} + \text{PPFD}_{\text{pLAI}})}$	$\text{PPFD}_{\text{pLAI}}, \text{PPFD}_{50}$	Photosynthetically active photon flux density per projected LAI, PPFD for half stomata closure
7	$g_{\text{trans}} = \frac{g_{\text{bl}} \cdot (g_s + g_c)}{(g_{\text{bl}} + g_s + g_c)}$	$g_{\text{trans}}, g_{\text{bl}}, g_c$	Leaf-level conductance, boundary layer conductance, cuticular conductance

conductance (g_s) and cuticular conductance (g_c) in parallel and boundary conductance (g_{bl} , Table 3) in series (Table 5, Eq. 7).

References

- Aigner J (1991) Wurzelraum eines sekundären Fichtenbestandes im tertiären Hügelland Oberösterreichs (Root zone of a secondary spruce stand in the tertiary hills of Upper Austria). Master thesis, University of Natural Resources and Life Sciences, Vienna
- Badoux A, Witzig J, Germann PF et al (2006) Investigations on the runoff generation at the profile and plot scales, Swiss Emmental. Hydrol Process 20:377–394. doi:10.1002/hyp.6056
- Beckers J, Smerdon B, Wilson M (2009) Review of hydrologic models for forest management and climate change applications in British Columbia and Alberta. FORREX, Kamloops, BC. FORREX Series Report No. 25

- Berger F, Rey F (2004) Mountain protection forests against natural hazards and risks: New French developments by integrating forests in risk zoning. *Nat Hazards* 33:395–404. doi:[10.1023/B:NHAZ.0000048468.67886.e5](https://doi.org/10.1023/B:NHAZ.0000048468.67886.e5)
- Bitterlich W (1948) Die Winkelzählprobe (The angle-count sample). *Allg Forst- und Holzwirtschaftszeitung* 59:4–5
- Bobeva A (2003) Quantifying the distribution of forest functional types and forest. PhD thesis, University Bayreuth
- Brang P, Schönenberger W, Ott E, Gardner B (2001) Forests as protection from natural hazards. In: Evans J (ed) *For. Handb.* Blackwell Science, Oxford, pp 53–81
- Clapp RB, Hornberger GM (1978) Empirical equations for some soil hydraulic properties. *Water Resour Res* 14:601–604. doi:[10.1029/WR014i004p00601](https://doi.org/10.1029/WR014i004p00601)
- Cosby BJ, Hornberger GM, Clapp RB, Ginn TR (1984) A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resour Res* 20:682–690. doi:[10.1029/WR020i006p00682](https://doi.org/10.1029/WR020i006p00682)
- Eastaugh CS, Pötzelsberger E, Hasenauer H (2011) Assessing the impacts of climate change and nitrogen deposition on Norway spruce (*Picea abies* L. Karst) growth in Austria with BIOME-BGC. *Tree Physiol* 31:262–274. doi:[10.1093/treephys/tpr033](https://doi.org/10.1093/treephys/tpr033)
- Engler A (1919) Untersuchungen über den Einfluß des Waldes auf den Stand der Gewässer (Studies on the influence of the forest on the state of waterbodies). *Mitteilungen der Schweizerischen Zentralanstalt für das forstliche Versuchswesen* 12
- Enting IG, Wigley TML, Heimann M, Scientific C (1994) Future emissions and concentrations of carbon dioxide: key ocean/atmosphere/land analyses. Division of Atmospheric Research Technical Paper no. 31. CSIRO, Australia
- Geitner C, Mergili M, Lammell J et al (2009) Modelling peak runoff in small Alpine catchments based on area properties and system status. In: Veulliet E, Johann S, Weck-Hannemann H (eds) *Sustainable natural hazard management in alpine environments.* Springer, Berlin, pp 103–134
- Gower ST, Kucharik CJ, Norman JM (1999) Direct and indirect estimation of Leaf Area Index, f APAR, and net primary production of terrestrial ecosystems. *Remote Sens Environ* 70:29–51
- Hagen K (2003) Wildbacheinzugsgebiet Schmittenbach (Salzburg)—Analyse des Niederschlags- und Abflussgeschehens 1977–1998 (Torrential Watershed of Schmittenbach (Salzburg)—Analysis of Precipitation and Runoff). *BFW Berichte* 129:101
- Hamilton L (1992) The protective role of mountain forests. *GeoJournal*. doi:[10.1007/BF00150632](https://doi.org/10.1007/BF00150632)
- Hasenauer H, Burgmann M, Lexer MJ (2000) Concepts within forest ecosystem modeling. *Cent für das gesamte Forstwes* 117:137–164
- Hasenauer H, Merganicova K, Petritsch R et al (2003) Validating daily climate interpolations over complex terrain in Austria. *Agric For Meteorol* 119:87–107. doi:[10.1016/S0168-1923\(03\)00114-X](https://doi.org/10.1016/S0168-1923(03)00114-X)
- Hinterstoisser H (1985) Die forstliche Problematik intensiver Wintersporterschließung am Beispiel der Schmittenhöhe, Zell am See (The silvicultural problem of intensive winter sports development on the example of the Schmittenhöhe, Zell am See). *Mitteilungen der Gesellschaft für Salzburg. Landeskunde, Salzburg*
- IPCC (1992) *Climate change 1992: the supplementary report to the IPCC scientific assessment.* Cambridge University Press, Cambridge
- Kilian W, Müller F, Starlinger F (1994) Die forstlichen Wuchsgebiete Österreichs (The Forest Ecoregions of Austria). *BFW-Berichte* 82:60
- Lange B, Germann PF, Lüscher P (2010) Einfluss der Wurzeln auf das Wasserspeicher vermögen hydromorpher Waldböden (Significance of roots for soil water storage capacity of hydromorphic forest soils). *Schweizerische Zeitschrift für Forstwes* 161:510–516
- Markart G, Kohl B, Perzl F (2006) Der Bergwald und seine hydrologische Wirkung - eine unterschätzte Größe? (The mountain forest and its hydrological function—an underestimated factor?). *LWF Wissen* 55:34–43
- Marschall J (1975) *Hilfstafeln für die Forsteinrichtung (Yield tables for forest planning).* Österreichischer Agrarverlag
- Merganičová K, Pietsch SA, Hasenauer H (2005) Testing mechanistic modeling to assess impacts of biomass removal. *For Ecol Manage* 207:37–57. doi:[10.1016/j.foreco.2004.10.017](https://doi.org/10.1016/j.foreco.2004.10.017)
- Merganičová K, Merganic J, Hasenauer H (2012) Assessing the carbon flux dynamics within Virgin forests. *Austrian J For Sci* 129:1–21
- Olschewski R, Bebi P, Teich M et al (2012) Avalanche protection by forests—a choice experiment in the Swiss Alps. *For Policy Econ* 15:108–113. doi:[10.1016/j.forpol.2011.10.002](https://doi.org/10.1016/j.forpol.2011.10.002)
- Pallardy SG (2008) *Physiology of woody plants*, 3rd ed. doi:[10.1016/B978-012088765-1.50015-4](https://doi.org/10.1016/B978-012088765-1.50015-4)

- Petritsch R (2008) Large scale mechanistic ecosystem modeling in Austria. PhD thesis, University of Natural Resources and Life Sciences, Vienna
- Petritsch R, Hasenauer H (2007) Interpolating input parameters for large scale ecosystem models. *Austrian J For Sci* 124:135–151
- Petritsch R, Hasenauer H (2014) Climate input parameters for real-time online risk assessment. *Nat Hazards* 70:1749–1762. doi:10.1007/s11069-011-9880-y
- Petritsch R, Hasenauer H, Pietsch SA (2007) Incorporating forest growth response to thinning within biome-BGC. *For Ecol Manage* 242:324–336. doi:10.1016/j.foreco.2007.01.050
- Pietsch SA, Hasenauer H (2002) Using mechanistic modeling within forest ecosystem restoration. *For Ecol Manage* 159:111–131. doi:10.1016/S0378-1127(01)00714-9
- Pietsch SA, Hasenauer H (2006) Evaluating the self-initialization procedure for large-scale ecosystem models. *Glob Chang Biol* 12:1658–1669. doi:10.1111/j.1365-2486.2006.01211.x
- Pietsch SA, Hasenauer H, Thornton PE (2005) BGC-model parameters for tree species growing in central European forests. *For Ecol Manage* 211:264–295. doi:10.1016/j.foreco.2005.02.046
- Placer K, Schneider J (2001) Arbeiten zur Kartierung der trockenen Deposition in Österreich (Studies on the mapping of dry deposition in Austria). Fed Environ Agency, Austria
- Pollanschütz J (1971) Auswertung von Waldinventur (Analysis of forest inventory). 100 Jahre Hochschule für Bodenkultur. Vienna, pp 355–368
- Reineke LH (1933) Perfecting a stand density index for even-aged forests. *J Agric Res* 46:627–638
- Reynolds MR (1984) Estimating the error in model predictions. *For Sci* 30:454–469
- Running SW (1992) A bottom-up evolution of terrestrial ecosystem modeling theory, and ideas toward global vegetation modeling. *Univ Corp Atmos Res Model Earth Syst* 3:263–280
- Saxton KE, Rawls WJ, Romberger JS, Papendick RI (1986) Estimating generalized soil–water characteristics from texture. *Soil Sci Soc Am J* 50:1031. doi:10.2136/sssaj1986.03615995005000040039x
- Schaffhauser H (1982) Untersuchungen über das Abflussverhalten verschieden bewirtschafteter Versuchsfelder (Studies on the outflow behaviour of differently managed experimental areas). *Mitteilungen der Forstl Bundesversuchsanstalt, Wien* 144:85–102
- Schmittenhöhebahn AG (2014) Skiing and snowboarding. <http://www.schmitten.at>. Accessed 26 March 2014
- Schneider J (1998) Kartierung der nassen Deposition in Österreich (Mapping of the wet deposition in Austria). Fed Environ Agency, Austria
- Sidle RC, Pearce AJ, O'Loughlin CL (1985) Hillslope stability and land use. *Water Resour Monogr*. 11. AGU, Washington, DC
- Sonnier J (1991) Analyse du rôle de protection des forêts domaniales de montagne (Analysis of the role of protecting the state mountain forests). *Rev For Française* 43:131–145
- Thoma R (1900) *Berichte des Forst-Vereins für Oberösterreich und Salzburg* (Reports of the forest association for Upper Austria and Salzburg), 40. Band. Forstverein für Oberösterreich und Salzburg, Gmunden
- Thornton PE (1998) Regional ecosystem simulation: combining surface- and satellite-based observations to study linkages between terrestrial energy and mass budgets. PhD thesis, University of Montana, Missoula
- Thornton PE, Running SW, White M (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251. doi:10.1016/S0022-1694(96)03128-9
- Thornton PE, Hasenauer H, White M (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric For Meteorol* 104:255–271. doi:10.1016/S0168-1923(00)00170-2
- Thornton PE, Law BE, Gholz HL et al (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric For Meteorol* 113:185–222. doi:10.1016/S0168-1923(02)00108-9
- Uddling J, Teclaw RM, Kubiske ME et al (2008) Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiol* 28:1231–1243
- Warren JM, Pötzelsberger E, Wullschlegel SD et al (2011) Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂. *Ecohydrology* 4:196–210. doi:10.1002/eco.173
- Wehrli A, Brang P, Maier B et al (2007) Schutzwaldmanagement in den Alpen—eine Übersicht (Management of protection forests in the Alps—an overview). *Schweizerische Zeitschrift für Forstwes* 158:142–156. doi:10.3188/szf.2007.0142
- White M, Thornton PE, Running SW, Nemani RR (2000) Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4:1–85. doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2

WLV (1996) Technischer Bericht des Flächenwirtschaftlichen Projektes Schmittbach (Technical report of the management project river Schmittbach). Wildbach- und Lawinenverbauung (WLV)—Forsttechnischer Dienst—Gebietsbauleitung Pinzgau, Zell am See

APPENDIX III

Warren, J.M., Pötzelsberger, E., Wullschleger, S.D., Thornton, P.E., Hasenauer, H., Norby, R., 2011. Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂. *Ecohydrology* 4:196–210.

Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂*

Jeffrey M. Warren,^{1,2*} Elisabeth Pötzelsberger,² Stan D. Wullschleger,¹ Peter E. Thornton,¹ Hubert Hasenauer² and Richard J. Norby¹

¹ Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

² Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

ABSTRACT

Plants influence ecosystem water balance through their physiological, phenological, and biophysical responses to environmental conditions, and their sensitivity to climate change could alter the ecohydrology of future forests. Here we use a combination of measurements, synthesis of existing literature, and modelling to address the consequences of climate change on ecohydrologic processes in forests, especially response to elevated CO₂ (eCO₂). Data assessed from five free-air CO₂ enrichment (FACE) sites reveal that eCO₂-reduced stomatal conductance led to declines in canopy transpiration and stand water use in three closed-canopy forest sites. The other two sites were in the early stages of stand development, where a strong eCO₂-stimulation of canopy leaf area led to enhanced stand water use. In the sweetgum FACE experiment in Oak Ridge, Tennessee (USA), eCO₂ reduced seasonal transpiration by 10–16%. Intra-annual peak measured fluxes in transpiration ranged from 4.0–5.5 mm day⁻¹, depending on year. The Biome-BGC model simulated similar rates of transpiration at this site, including the relative reductions in response to eCO₂. As a result, simulations predict ~75 mm average annual increase in potential water yield in response to eCO₂. The direct effect of eCO₂ on forest water balance through reductions in transpiration could be considerable, especially following canopy closure and development of maximal leaf area index. Complementary, indirect effects of eCO₂ include potential increases in root or leaf litter and soil organic matter, shifts in root distribution, and altered patterns of water extraction. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS climate change; FACE; global change; sap flow; streamflow; transpiration

Received 25 January 2010; Accepted 7 October 2010

INTRODUCTION

The terrestrial water cycle functions across multiple spatial and temporal scales, simultaneously driven by dynamics of water transport vertically through the soil–plant–atmosphere continuum and horizontally across the landscape (Chahine, 1992; Loaiciga *et al.*, 1996; Rodriguez-Iturbe, 2000). Ecosystems, in turn, respond to the resulting soil and topographic conditions created by the vertical and horizontal flux of water and exert an influence on the hydrologic cycle through feedbacks that are driven by the distribution, structure, function, and dynamics of plant communities (Newman *et al.*, 2006). In addition, water use within and movement from ecosystems is strongly regulated by component interactions between soils and plants in response to climatic and edaphic factors (Jackson *et al.*, 2001; Newman *et al.*,

2006). Local, regional, and global water cycles are therefore likely to be sensitive to current and projected changes in climate including warmer temperatures, altered precipitation patterns, and rising CO₂ concentrations in the atmosphere (Cramer *et al.*, 2001; Thornton *et al.*, 2002; Gerten *et al.*, 2004; Meehl *et al.*, 2007).

Research conducted on the response of woody vegetation to climate change, in particular, to atmospheric CO₂ enrichment, has revealed the sensitivity of several key plant processes to elevated CO₂ (eCO₂). The most prominent of these has been that the eCO₂ can lead to higher leaf photosynthesis, a general stimulation of net canopy carbon uptake, and enhanced rates of net primary production (NPP)—with the potential for increased carbon storage in terrestrial ecosystems (Norby *et al.*, 2005; Leakey *et al.*, 2009). There is an equally strong expectation that the CO₂-induced reductions in stomatal conductance and leaf-level transpiration may have important consequences for forest water dynamics (Betts *et al.*, 2007; Leuzinger and Körner, 2010) and, in turn, for ecosystem-scale processes that depend on soil water availability.

Although the leaf-level responses of stomatal conductance to eCO₂ are important, they are by themselves insufficient to draw conclusions about ecohydrological processes that operate at longer and larger temporal and spatial scales (Wullschleger *et al.*, 2002b). eCO₂ can

*Correspondence to: Jeffrey M. Warren, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6442 USA. E-mail: warrenjm@ornl.gov

*“Notice: This manuscript has been authored by UT-Battelle, LLC, under Contract No. DE-AC05-00OR22725 with the U.S. Department of Energy. The United States Government retains and the publisher, by accepting the article for publication, acknowledges that the United States Government retains a non-exclusive, paid-up, irrevocable, world-wide license to publish or reproduce the published form of this manuscript, or allow others to do so, for United States Government purposes”.

increase carbon allocation below ground, thereby increasing root biomass, shifting root distribution within the soil profile, and potentially increasing build-up of soil organic matter (SOM) through root turnover and exudation (Jastrow *et al.*, 2005; Iversen *et al.*, 2008). Root distribution, production, and turnover can affect water infiltration dynamics because of the influence of root channels and preferential pathways of water transport within the profile. Additional organic matter inputs to the soil can increase the soil water-holding capacity and buffer water release and flows within the vadose zone. Interactions among root distribution, SOM, and soil water content will impact seasonal timing and depth of water extraction, and thereby apparent water stress (and carbon uptake) during the growing season. Integrated consideration of soil–root and leaf–atmosphere responses to changes in CO₂ availability (Wullschleger *et al.*, 2002a) must be scaled to impacts realized at canopy and landscape levels to ultimately address higher-order questions about forest water use and potential water conservation on ecosystem-scale processes.

A larger-scale, longer-term consideration of shifts in vegetation structure may then be linked to species-specific competitive interactions within ecosystems in response to the changing environment, such as woody plant expansion or contraction from specific landscapes.

Achieving an integrated understanding of how climate change will impact hydrologic cycles in forests will require a concerted effort. It is, however, an important goal and one that can best be addressed through an approach that engages experimentalist and modeller. There have been a variety of modelling efforts to assess the impacts of changing environmental conditions on ecosystem water use (Law *et al.*, 2000; Hanson *et al.*, 2005; Siqueira *et al.*, 2006; Luo *et al.*, 2008) that vary widely in their spatial scale and temporal time step. Ecosystem water flux is often linked to individual environmental constraints to stomatal conductance (e.g. radiation and vapour pressure deficit (VPD); Ewers *et al.*, 2005), maintenance of hydraulic conductance through the soil–plant–atmosphere continuum (Sperry *et al.*, 1998), and various measures and estimates of site water balance (Wilson *et al.*, 2001; Schäfer *et al.*, 2002; Warren *et al.*, 2005; Granier *et al.*, 2007; Leuzinger and Körner, 2010). As issues that surround the response of forests to climate change become more complex, additional studies that integrate across temporal and spatial scales will be required.

In this study, we use a combination of analysis of experimental data, synthesis of existing literature, and modelling to address the mechanisms and implications of climate change on ecohydrologic processes in forests. Research conducted over the last 12 years at the Oak Ridge National Laboratory (ORNL) free-air CO₂ enrichment (FACE) facility highlights the role of leaf- and canopy-scale processes in determining the hydrologic response of forests to climate change. Information from these investigations coupled with published results from

other forest FACE experiments are used to parameterize the Biome-BGC model (Thornton *et al.*, 2002), an ecosystem process model that simulates water, energy, and biogeochemical fluxes on a daily time step. Model mechanisms controlling site water balance are evaluated against long-term measurements, and predictive ecohydrological responses to atmospheric CO₂ enrichment are explored at the landscape scale.

MATERIALS AND METHODS

Comparative CO₂ enrichment studies

Ecohydrological impacts of woody plant response to eCO₂ have long been inferred from measurements conducted on single leaves, seedlings, or individual saplings grown in growth chambers, greenhouses, or open-top outdoor chambers (Norby *et al.*, 1999). While they are useful for the recognition of potential physiological responses to eCO₂ like photosynthesis (Wullschleger *et al.*, 1992), the size and longevity of forests generally precluded investigations of stand-level responses. In addition, the artificial nature of these enclosed systems can easily confound results of CO₂ treatments, driven by concurrent alterations in the localized plant environment and interactive feedbacks; e.g. spectral quality, thermal gradients, wind, moisture availability, soil characteristics, or rooting depth. Accurate measurement and modelling of eCO₂-dependent water flux dynamics under natural conditions and at larger spatial and temporal scales has thus required a substantial shift in the experimental systems (Norby *et al.*, 2001). As such, FACE technology has been employed, void of chamber walls and permitting plots that were large enough such that the experiments were not limited to seedlings, single trees, or clusters of small-stature individuals. FACE studies in woody ecosystems began in earnest in the 1990s, with some studies continued for a decade or longer, exposing maturing stands to inter-annual climate variations in conjunction with regulated CO₂ concentrations. Here, we consider five long-term FACE studies that have been conducted in temperate forest ecosystems, with plantations of young poplar (treatments applied as trees aged 0–6 years, coppiced at year 3; POP/EuroFACE), aspen/birch/maple (0–12 years; Aspen-FACE), pine (14–27 years; Duke), sweetgum (12–21 years; ORNL), and mature mixed hardwood (~100 years; Web-FACE). Ecohydrological data from these five sites comprised the comparative literature review (Table I), with measurement and modelling of the sweetgum plantation at ORNL used as a case study (described below).

ORNL site description and experimental facilities

The research reported here, much of which spans the period 1998–2008, took place in a 12- to 21-year-old sweetgum (*Liquidambar styraciflua* L.) tree plantation established in Oak Ridge National Environmental Research Park in eastern Tennessee (35°54'N;

Table I. Physiological and hydrological responses of trees and forests to atmospheric CO₂ enrichment.

Parameter	Web-FACE	Duke	ORNL	Aspen-FACE	POP/EuroFACE
Stomatal conductance	−4 to −21	−5	−14 to −44	0 to −44/+19	−16 to −39
Stand water use	−14	−7	−13	+25	+12 to +23
Evapotranspiration	−10	na	−7	na	na
Runoff	na	+	na	na	na
Drainage	na	+	na	na	na
Upper soil moisture	0/+	+	0/+	+	na
Root production	na	+	+	0/+	+
Root standing crop	0/−	+	+	+	+
LAI	0	0/+	0/+	+	+
Species	<i>Carpinus betulus</i>	<i>Pinus taeda</i>	<i>Liquidambar styraciflua</i>	<i>Populus tremuloides</i>	<i>Populus x euramericana</i>
	<i>Fagus sylvatica</i>	—	—	<i>Betula papyrifera</i>	—
	<i>Quercus petraea</i>	—	—	<i>Acer saccharum</i>	—
References	Cech <i>et al.</i> (2003)	Ellsworth <i>et al.</i> (1995)	Gunderson <i>et al.</i> (2002)	Noormets <i>et al.</i> (2001)	Liberloo <i>et al.</i> (2005)
	Keel <i>et al.</i> (2007)	Ellsworth (1999)	Norby <i>et al.</i> (2003)	Uddling <i>et al.</i> (2008, 2009)	Lukac <i>et al.</i> (2003)
	Leuzinger <i>et al.</i> (2005)	McCarthy <i>et al.</i> (2007)	Wullschleger and Norby (2001)		Tricker <i>et al.</i> (2005)
	Leuzinger and Körner (2007)	Pritchard <i>et al.</i> (2008)	Wullschleger <i>et al.</i> (2002b)	King <i>et al.</i> (2005)	Tricker <i>et al.</i> (2009)
	Bader <i>et al.</i> (2009)	Schäfer <i>et al.</i> (2002)	Iversen <i>et al.</i> (2008)	Pregitzer <i>et al.</i> (2008)	—

Quantitative and qualitative estimates were derived from the published literature for long-term studies where trees were exposed to ambient and *ca* 550 ppm CO₂ concentrations. Values represent the percentage change in a variable in response to eCO₂. Non-measured values are represented by 'na'.

84°20'W), at an elevation of 227 m. One-year-old sweetgum seedlings were planted in 1988 at 2.3 × 1.2 m spacing on previously cultivated alluvial land along the Clinch River. The soil is an Aquic Hapludult with a silty-clay-loam texture (21:55:24; sand:silt:clay). Rooting depth was ~1.2–2.2 m for individual sweetgum trees destructively extracted from the site after conclusion of the study (Warren *et al.*, unpublished). A survey of the site in 1998 indicated that the 10-year-old plantation had a basal area of about 29 m² ha^{−1} with an average height of 12 m and an average leaf area index (LAI) of 5.5 m² m^{−2}.

A FACE system was installed in four of the five 25-m diameter plots in 1997. The FACE system regulates the release of CO₂ from the vertical PVC vent pipes located around each plot on the basis of wind speed, wind direction, and *in situ* measurements of current CO₂ concentration within the canopy (Hendrey *et al.*, 1999). Since 1998, eCO₂ has been released into the two treatment plots during each growing season, while the tree stands in the other three plots were in air with the current ambient CO₂ (aCO₂) concentration. Atmospheric CO₂ in the elevated plots was maintained at a target daytime concentration of 525–555 ppm during the growing season, *ca* 40% higher than CO₂ levels in the ambient plots (380–400 ppm).

Mean annual temperature (1962–1993) at the study site is 13.9°C and the annual precipitation averages 1371 mm. Precipitation is generally distributed throughout the year at the site; however, there are often 3- to 5-week periods of significant water deficit during late summer. Volumetric soil water content in the upper

soil (0–20 cm) was measured at six locations per plot throughout the growing season using time-domain reflectometry (Soil Moisture Equipment Corporation, Santa Barbara, CA, USA). Climate data were collected in all years with micrometeorological equipment including measurement of precipitation, wind, photosynthetically active radiation (PAR), and air temperature and relative humidity above and beneath the canopy. All micrometeorological data are documented and archived for public use at http://public.ornl.gov/face/ORNL/ornl_data.shtml.

Measured sap flow and canopy transpiration

The compensated heat-pulse technique (Greenspan Technology Pty. Ltd, Warwick, Queensland, Australia) was used in 1999 and 2004 to measure the sap flow for four trees in each of two aCO₂ and eCO₂ plots (16 trees in total). These trees were located near the centre of each plot and ranged in diameter from 12.4 to 14.7 cm in 1999 and 11.4 to 19.8 cm in 2004. A single heat-pulse probe was positioned in each tree so that the sensing thermistor was located at a sapwood depth of 19 mm. The control module and data logger were programmed to provide a heat pulse for 1.8 s and measurements were recorded every 60 min. Sap velocity was calculated from the corrected heat-pulse velocity based on Equation 3 of Barrett *et al.* (1995). All other aspects of data analysis are described in Wullschleger and Norby (2001).

Sap flow in 2008 was quantified using thermal dissipation probes (Dynamax Inc., Houston, TX, USA) installed at multiple depths in five trees in each of the two aCO₂ and two eCO₂ treatment plots. These trees were located across each plot and ranged in diameter (DBH) from 13.2

to 22.4 cm. As described by Granier (1987), the temperature difference between the heated and unheated probe is proportional to the voltage differential between the probes and can be related to sap velocity based on the empirical relationship between the voltage differential and the heat dissipation attributable to sap flow near the heated probe. Probes were insulated with polystyrene foam and reflective bubble insulation to minimize errors due to natural thermal gradients. Voltage differences between probes were sampled every 15 min during the growing season and stored on a data logger (model CR10X, Campbell Scientific). Radial patterns of sap flow were established using measurements of sap velocity at 1.5, 2.5, and 7.0 cm within dominant trees. Tree sap flow was calculated by linear interpolation of radial patterns of sap velocity through each consecutive annulus of sapwood area bound by sensors installed at different depths.

Hourly rates of stand transpiration (mm h^{-1}) for each of the two aCO₂ and two eCO₂ plots were estimated as a function of measured sap velocity, total stand sapwood area, and the fraction of sapwood functional in water transport. Sapwood area averaged across all plots was 23.7 m² ha⁻¹ in 1999 (Wullschleger and Norby, 2001), 30.5 m² ha⁻¹ in 2004, and 36.3 m² ha⁻¹ in 2008. Treatment differences in sapwood area were not observed over the course of the experiment. Daily rates of stand transpiration (mm day^{-1}) in both the years were calculated via a simple summation of hourly rates.

Model description

We used the terrestrial ecosystem process model Biome-BGC, version 4.1.1 (Thornton *et al.*, 2002), incorporating an extension on the model self-initialization that uses a dynamic mortality routine (Pietsch and Hasenauer, 2006). The Biome-BGC model simulates states and fluxes of water, carbon, and nitrogen in a forest ecosystem, using a daily time step. The model is forced by daily weather data: minimum and maximum near-surface air temperature, incident shortwave radiation, atmospheric VPD, and precipitation. These were calculated from hourly observations made at the site from 1998 to 2008 (Riggs *et al.*, 2009). Other required model inputs include ecophysiological parameters, disturbance history, soil physical properties, atmospheric CO₂, and atmospheric nitrogen deposition.

The plant canopy LAI controls canopy radiation absorption and light transmission to the ground, water interception in the canopy, photosynthesis, and litter inputs to the detrital pools. Timing of the canopy development and senescence is dependent on temperature and day length following the approach of White *et al.* (1999), and ultimately constrains seasonal patterns of photosynthesis and transpiration. Photosynthesis is calculated with the Farquhar photosynthesis routine using kinetic constants as per Woodrow and Berry (1988); and de Pury and Farquhar (1997), as well as parameters defined by Kuehn and McFadden (1969); and Wullschleger (1993), and a $V_{\text{max}}-J_{\text{max}}$ relationship specifically described for ORNL

FACE (Sholtis *et al.*, 2004). The model is sensitive to feedbacks from mineralization processes and thus site nutrient availability. The model also depends heavily on water inputs and cycling through the ecosystem. Precipitation is partially intercepted by the canopy, depending on the LAI, an interception coefficient, and the precipitation intensity; and the residual is input directly to the soil water pool. The canopy water either evaporates on the same day or, if not all the intercepted water can be evaporated, is added to the soil water pool, to represent canopy dripping. Evaporation is calculated independently from the leaf and the soil surfaces with the Penman–Monteith equation as a function of air temperature, air pressure, VPD, incident solar radiation, and the transport resistance of water vapour and sensible heat. The model assumes a single canopy layer, and does not assess the potential contribution from the relatively sparse understorey. Precipitation inputs to the soil water pool can drain as outflow (water yield) or be stored and available for evaporative or transpirational loss from the system. The total soil water–holding capacity at saturation is determined from the total ‘effective soil depth’ and texture based on empirical pedotransfer functions (Clapp and Hornberger, 1978; Cosby *et al.*, 1984; Saxton *et al.*, 1986). Effective soil depth for both treatments was defined as 2 m, derived from the maximum observed rooting depth and reduced by the estimated stone fraction >2 mm. Subsequent model estimation of soil water potential was modified to fit the soil water retention curve previously developed for the Oak Ridge FACE site (Warren *et al.*, unpublished).

Potential water yield from the system requires knowledge of volumetric water content at field capacity, defined here as -0.033 MPa on the basis of field data collected at the Oak Ridge FACE site. The model assumes that water above saturation is lost immediately as outflow and that water between saturation and field capacity is lost at a rate of 50% per day. Remaining soil water is then available for evapotranspiration. Plant water uptake is driven by the demand of water for transpiration, where transpiration is regulated by stomatal conductance and, as evaporation, calculated with the Penman–Monteith equation. Maximum stomatal conductance is limited by reduction factors, dependent on solar radiation, VPD, water potential gradients, and temperature. The stomata response to solar radiation is described as a hyperbolic function, with the half saturation value generally set to $75 \mu\text{mol m}^{-2} \text{s}^{-1}$ after Körner (1995) who gives a range of values between 50 and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. The other reduction factors are linear functions of the VPD, the soil water potential (a surrogate for the predawn leaf water potential), and the daily minimum temperature. Beyond certain threshold values, stomatal conductance is at its maximum or is zero (Table II). Total canopy conductance follows the electrical circuit analogy, with stomatal and cuticular conductance in parallel and leaf boundary layer conductance in series.

The model theory and its assumptions and methods of parameterization have been fully described elsewhere

Table II. Ecophysiological constants used in the Biome-BGC model of *Liquidambar styraciflua* as simulated under ambient (a) or elevated (e) atmospheric CO₂ as parameterized for the ORNL FACE research facility.

Parameter estimate		Unit	Parameter description	
eCO ₂	aCO ₂			
1	1	flag	1 = woody	0 = non-woody
0	0	flag	1 = evergreen	0 = deciduous
1	1	flag	1 = C3 photosynthesis	0 = C4 photosynthesis
1	1	flag	1 = model the phenology	0 = user-specified phenology
0	0	yday	Yearday to start new growth (when phenology flag = 0)	
0	0	yday	Yearday to end litter fall (when phenology flag = 0)	
0.2	0.2	—	Transfer growth period as fraction of growing season ^a	
0.3	0.3	—	Litter fall as fraction of growing season ^a	
1	1	yr ⁻¹	Annual leaf and fine-root turnover fraction ^b	
0.7	0.7	yr ⁻¹	Annual live wood turnover fraction ^b	
0.005	0.005	yr ⁻¹	Annual whole-plant minimum mortality fraction ^a	
0.02	0.02	yr ⁻¹	Annual whole-plant maximum mortality fraction ^a	
225	225	yr	Length for (low) elliptic mortality ^a	
75	75	yr	Length for (high) elliptic mortality ^a	
0	0	yr ⁻¹	Annual fire mortality fraction ^c	
0.72	0.38	—	(allocation) new fine root C : new leaf C ^c	
2.49	2.44	—	(allocation) new stem C : new leaf C ^c	
0.16	0.16	—	(allocation) new live wood C : new total wood C ^b	
0.07	0.08	—	(allocation) new coarse root C : new stem C ^c	
0.1	0.1	—	(allocation) current growth : storage growth ^c	
33	30	kg C kg ⁻¹ N	C : N of leaves ^c	
67	58	kg C kg ⁻¹ N	C : N of leaf litter ^c	
44	44	kg C kg ⁻¹ N	C : N of fine roots ^c	
50	50	kg C kg ⁻¹ N	C : N of live wood ^b	
434	430	kg C kg ⁻¹ N	C : N of dead wood ^c	
0.38	0.38	—	Leaf litter labile proportion ^b	
0.44	0.44	—	Leaf litter cellulose proportion ^b	
0.18	0.18	—	Leaf litter lignin proportion ^b	
0.34	0.34	—	Fine-root labile proportion ^b	
0.44	0.44	—	Fine-root cellulose proportion ^b	
0.22	0.22	—	Fine-root lignin proportion ^b	
0.77	0.77	—	Dead wood cellulose proportion ^b	
0.23	0.23	—	Dead wood lignin proportion ^b	
0.005	0.005	LAI ⁻¹ d ⁻¹	Canopy water interception coefficient ^a	
0.54	0.54	—	Canopy light extinction coefficient ^b	
2	2	—	All sided: projected leaf area ^b	
23.6	25	m ² kg ⁻¹ C	Canopy average specific leaf area (projected area basis) ^c	
1.26	1.26	—	Shaded: sunlit specific leaf area ^c	
0.12	0.12	—	Fraction of leaf N in Rubisco ^a	
0.0045	0.005	m s ⁻¹	Maximum stomatal conductance (projected area basis) ^d	
0.00006	0.00006	m s ⁻¹	Cuticular conductance (projected area basis) ^b	
0.01	0.01	m s ⁻¹	Boundary layer conductance (projected area basis) ^b	
-0.334	-0.334	MPa	Leaf water potential: start of conductance reduction ^b	
-2.2	-2.2	MPa	Leaf water potential: complete conductance reduction ^b	
500	500	Pa	VPD: start of conductance reduction ^d	
3600	3600	Pa	VPD: complete conductance reduction ^b	
0	0	°C	Night temperature: start of conductance reduction ^b	
-8	-8	°C	Night temperature: complete of conductance reduction ^b	

Parameter differences between CO₂ treatments are in bold.

^a E. Pötzelsberger, personal assessment.

^b White *et al.* (2000).

^c Published data from the ORNL FACE site: http://public.ornl.gov/face/ORNL/ornl_data.shtml.

^d Wullschleger *et al.* (2002b).

(White *et al.*, 2000; Thornton *et al.*, 2002; Thornton and Rosenbloom, 2005; Pietsch and Hasenauer, 2006).

Application of Biome-BGC to the ORNL FACE site

In this study, our aim was to (1) represent observed growth and water use of the ORNL FACE plots from

1998 to 2008 using the mechanistic ecosystem model Biome-BGC, (2) quantify non-measured ecosystem water fluxes, and (3) determine treatment-specific ecosystem water budgets. The model was informed by measurements within two eCO₂ plots or three aCO₂ plots, scaled to one simulation per treatment. Parameters were based

on site measurements, previous values used at similar sites, or informed estimates (Table II). Daily weather data were assumed to be constant across treatments, and included daily minimum and maximum temperatures, precipitation, relative humidity and total incident radiation, and albedo (assumed at 0.2). Differences between the two simulated ecosystems lay in some of the ecophysiological constants derived from measurements at the site, and, of course, the atmospheric CO₂ content.

A total of 42 ecophysiological parameters were required for the vegetation-specific parameterization (Table II), many of which were available from previous measurements at the ORNL FACE site. Parameters associated with carbon (C) and nitrogen (N) allocation within the various plant compartments were based on allometric relationships (Norby *et al.*, 2002). C allocation has shifted through time at the site, such that fine root:leaf, coarse root:stem, and stem:leaf allocation ratios declined over the years of the experiment; however, the model does not allow dynamic allocation parameters. Similarly, plant tissue C:N ratios that regulate respiration, and determine, for leaves, the maximum rate of carboxylation (V_{cmax}), show a positive trend over the years. In addition, the canopy-averaged specific leaf area declined through time. While there were multiple processes and components of the system that were dynamic, the limitations in this version of the model required some parameters to be based on mean values over the entire observation period.

Maximum stomatal conductance is a particularly important ecophysiological parameter for the water budget, and is greatly reduced by eCO₂ treatments. As described earlier, the model can reduce stomatal conductance based on the reduction factors associated with several environmental variables. The model assumes a linear relationship between stomatal conductance (g_s) and VPD between a lower (where g_s reduction begins) and an upper boundary (where stomata closure is complete). The lower boundary (0.5 kPa) could be estimated from canopy conductance—VPD data obtained in 1999 (Wullschleger *et al.*, 2002b). Stomatal response to atmospheric CO₂ concentration, however, has not yet been explicitly addressed in the model. In order to account for reduced stomata aperture under eCO₂, a lower maximum value for stomatal conductance was set—equal to 0.0045 m s⁻¹ (eCO₂) as compared to 0.005 m s⁻¹ (aCO₂)—based on canopy conductance estimates derived from sap flow measurements using an inverted Penman–Monteith equation (Wullschleger *et al.*, 2002b).

The Biome-BGC model was first parameterized to fit the average stand situation between 1999 and 2008, and then run for the whole time period to assess its applicability for prediction of canopy transpiration and site water fluxes until 2008. Several problems arose with the parameterization. First, simulated spring initiation of the canopy occurred several weeks earlier than observed leaf out. The sweetgum trees were established from a more northerly seed source (Missouri) and have always displayed bud-burst later than native vegetation. Thus, the

seasonal development of simulated LAI for the model had to be adjusted by altering the empirical formulation of White *et al.* (1999) and hence shifting the day of leaf flushing by more than two weeks. Second, the soil water retention properties modelled using the empirical pedotransfer formulations of Clapp and Hornberger (1978); Saxton *et al.* (1986), and Cosby *et al.* (1984) did not match field observations. At a given volumetric water content, the soil water potential was underestimated (more negative) and thus drought stress and attendant reductions in stomatal conductance appeared too early in the simulations. Slight modifications of the original formulations significantly improved the model performance with regard to the transpiration predictions, especially during periods of limited water supply. Thus, premature complete stomatal closure (which was not observed) due to low soil water potential could be avoided in the model. Modifications included adjustment of the modelled water retention curve to better reflect field measurements and adjustment of relative maximum stomatal conductance between treatments—differences in field measurements (Wullschleger *et al.*, 2002b) varied from 0–20+%, a value of 10% was settled on for the simulations which provided the best fit to the data. Variability in the tree size and structure can also affect the ability of the model to derive outflow from tree-level transpiration scaled to the stand. These include specifically variation in tree size, canopy position, stand-level, and microsite topography (including subsurface clay ‘lenses’), and seasonal dynamics of the coarse and fine litter layers. Each of these components is not directly included in the model, but may impact interception, evaporation, infiltration, and surface or subsurface flow dynamics.

RESULTS

Overview of FACE studies

eCO₂ consistently reduced the stomatal conductance by up to 44% across the five FACE studies (Table I), although in later years at Aspen-FACE eCO₂ had little effect or stimulated stomatal conductance (Uddling *et al.* 2009). Reduced stomatal conductance led to a decline in stand water use for sites that did not have a strong stimulation of LAI. Response of LAI within the pine FACE site was linked to soil nutrient availability, although inter-annual environmental conditions, especially drought, limited this response (McCarthy *et al.*, 2007). Similarly at ORNL, eCO₂ tended to transiently increase sweetgum LAI during non-drought years, but not during drought and post-drought years (Norby *et al.*, 2003; Warren *et al.*, in review). In contrast, LAI and aboveground production were greatly enhanced by eCO₂ for *Populus* sp. in the Aspen-FACE and POP/EuroFACE studies, which resulted in substantial increases in stand water use. Despite some differences in LAI and stand water use among the FACE studies, eCO₂ increased water content in the upper 20 cm of the soil profile within the four non-irrigated FACE studies (Table I).

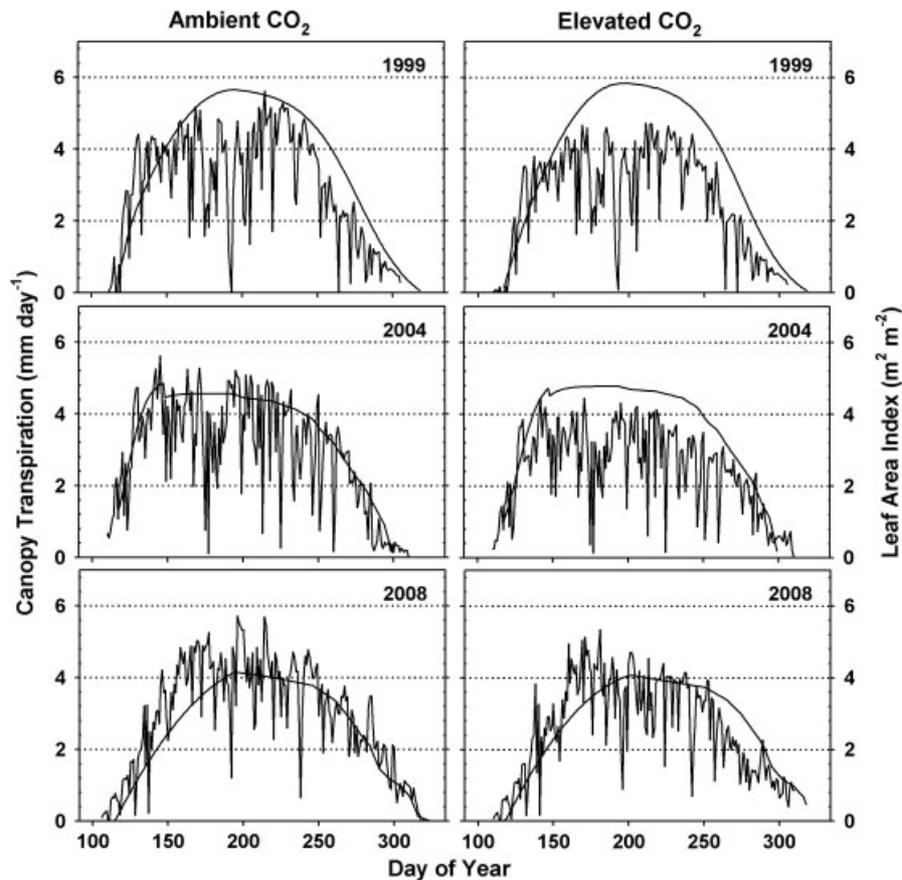


Figure 1. Daily canopy transpiration as scaled tree sap flow in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO₂ across multiple years. Seasonal patterns of leaf area index (LAI) were based on three aCO₂ plots or two eCO₂ plots (smooth lines), derived from Norby *et al.* (2003); Norby and Tharp (2008).

Root production and root standing crop were enhanced in response to eCO₂ for the young tree plantations (although not for older trees at the Web-FACE site) (Table I). There were large seasonal and inter-annual shifts in the magnitude of root responses to eCO₂; however, increased carbon allocation to the eCO₂ roots has been maintained through time across the four young FACE studies. In addition, there was substantial evidence of fine or coarse root distribution shifting deeper (>15 cm) with the soil profile at three of the FACE sites (Lukac *et al.*, 2003; Iversen *et al.*, 2008; Pritchard *et al.*, 2008); rocky subsoil limited depth of measurements at Web-FACE, and there are no reports of distribution shifts at Aspen-FACE.

Transpiration at ORNL FACE

Canopy transpiration of sweetgum trees in the ORNL case study was sampled in years 2, 6, and 10. Inter-annual transpiration remained fairly constant through time, with intra-annual peak fluxes reaching 4.0–5.5 mm day⁻¹ (Figure 1). The average response of plots exposed to eCO₂ during mid summer (June, July, and August) was a 7–16% reduction in transpiration, depending on year. eCO₂ reduced annual canopy transpiration by 10–16% (Table III). Variation in annual transpiration and eCO₂:aCO₂ (E:A) response was attributable to wind storms, drought, and other environmental stressors.

Canopy development and duration can provide some insight into the dynamics of plant water use; however, the magnitude of regulation may be overshadowed by other processes. In 1999, maximum LAI reached 5.7–5.8 (Figure 1), similar to other non-drought years. In 2004, a windstorm damaged the canopies of trees in both treatments, as illustrated by the abrupt stabilization in LAI by late May, one month earlier than other years (Figure 1). In 2008, LAI was the lowest as the study was initiated, driven by interactions between the 2007 drought and N limitations. Inter-annual peak LAI for aCO₂ was highly conserved during eight of the ten years without extreme events (5.60 ± 0.04), while peak LAI for eCO₂ plots remained much more variable (5.85 ± 0.17). Despite the differences in external environmental conditions and their effect on LAI, canopy transpiration was relatively constant over the lifetime of the experiment; inter-annual variation in both treatments was <10%.

eCO₂ treatments consistently reduced canopy transpiration by 10–15%, with the greatest effects on site water balance occurring when water use was greatest (Figure 2). For example, as transpiration in aCO₂ plots reached 4 mm day⁻¹, eCO₂ plots used only ~3.5 mm day⁻¹. Similarly, there was little difference in absolute transpiration between treatments as water use declined below 1 mm day⁻¹. The linear relationship between eCO₂ and aCO₂ treatments was not significantly

Table III. Seasonal and inter-annual patterns of measured and simulated canopy transpiration in a sweetgum forest exposed to long-term CO₂ treatments.

Year	CO ₂ treatment	Canopy Transpiration (mm d ⁻¹) (mm yr ⁻¹)							E : A	E : A
		Measured values	May	June	July	August	September	October		
1999	Ambient	3.4	3.7	3.5	4.4	2.6	1.0	568	0.90	0.93
	Elevated	2.8	3.4	3.2	3.9	2.5	0.8	511	—	—
2004	Ambient	3.6	3.6	3.9	3.5	2.8	0.9	576	0.85	0.84
	Elevated	2.9	3.0	3.2	3.0	2.3	1.2	487	—	—
2008	Ambient	2.2	4.3	4.1	4.0	3.3	1.9	622	0.84	0.88
	Elevated	2.0	4.0	3.5	3.4	2.5	1.2	522	—	—
Modeled values										
1999	Ambient	3.7	3.7	3.4	4.0	3.3	1.4	614	0.85	0.85
	Elevated	3.1	3.2	2.9	3.4	2.8	1.1	521	—	—
2004	Ambient	2.7	3.1	3.4	3.2	2.8	1.2	507	0.84	0.85
	Elevated	2.3	2.7	2.9	2.7	2.3	1.0	428	—	—
2008	Ambient	2.5	4.2	3.9	3.7	3.2	1.6	589	0.87	0.87
	Elevated	2.1	3.7	3.4	3.2	2.8	1.4	511	—	—

Annual fluxes include values from April to November during leaf development and leaf abscission. Transpiration ratio of eCO₂ to aCO₂ (E : A) is calculated annually and for mid-season fully developed canopies.

different through time. A linear regression across years suggests a consistent 14.6% reduction in transpiration from eCO₂ plots ($R^2 = 0.93$, $n = 596$).

Modelling ORNL FACE

Simulated inter-annual LAI peaked at ~ 4 for eCO₂ and between ~ 4 and 4.5 for aCO₂. In contrast, measured maximum LAI ranged from 4 to 6 for eCO₂ and from 4 to 5.8 for aCO₂. The shape of the simulated LAI curve differed from observations, increasing throughout the summer to a peak in mid-September (Figure 3), two months later than the observed peak (Figure 1).

As expected, once the model was parameterized, the simulated canopy transpiration tracked measured transpiration quite well (Figure 4). Seasonal initiation of transpiration, peak values, and response to environmental conditions were similar for measured and modelled values. There was a two week delay in the simulated seasonal decline in transpiration; measured transpiration declined by day of year (DOY) 245, while simulated transpiration declined by DOY 260 (Figure 5). Even so, the model (driven by day length) accurately terminated transpiration in early November.

As the model was projected forward through time, simulated canopy transpiration was tightly grouped around actual measured values (Figures 4 and 5). The correlation between simulated and measured values was maintained through 2008, especially from June to August (DOY 152–243) when simulated transpiration was 96 and 98% (eCO₂ and aCO₂, respectively; $s. e. \pm 1\%$) of measured transpiration. In May, 2008, the simulations overestimated transpiration by 8% (eCO₂) and 13% (aCO₂). In 2008, from September to October, the simulations underestimated transpiration for aCO₂ by 5%, and overestimated transpiration for eCO₂ by 16% (Figure 5).

Biome-BGC was able to partition fluxes among different ecohydrological components on the basis of

site water balance equations linked to simulated estimates of water flux. Precipitation inputs were balanced by evapotranspiration and soil water flow outputs. Water lost from the system via transpiration was a large component of simulated site water flux (Figure 6). The significant, long-term reduction in simulated eCO₂ transpiration agreed with the measured values through time. As a result, simulated water yield (surface runoff for saturated conditions and subsurface flow and drainage for unsaturated conditions) was significantly enhanced ($\sim 16\%$; $s. e. \pm 3\%$) by eCO₂. Potential water yield was 42 and 48% (aCO₂ and eCO₂) of annual precipitation at the site. The simulated eCO₂ ecosystem increased potential water yield by ~ 75 mm annually ($s. e. \pm 10$ mm), released during the growing season. Treatment differences in inter-annual values of outflow (eCO₂–aCO₂) ranged from 58 to 137 mm, except for the year 2007 in which there was no difference in modelled outflow. This was an extraordinarily dry and hot year, which led to premature leaf senescence across the stand (Warren *et al.*, In Review), and Biome-BGC was not able to accurately model transpiration—values were overestimated by 20–40%.

DISCUSSION

Regulation of stand water use

Our studies show, both experimentally and through the use of a model, that reductions in the stomatal conductance due to eCO₂ can affect leaf, plant, and ecosystem water use. The ecohydrologic consequences are manifested in increased site water yield. In addition, reduced ecosystem transpiration under eCO₂ will reduce regional-scale atmospheric humidity and thereby enhance the VPD (and driving force for water loss) between

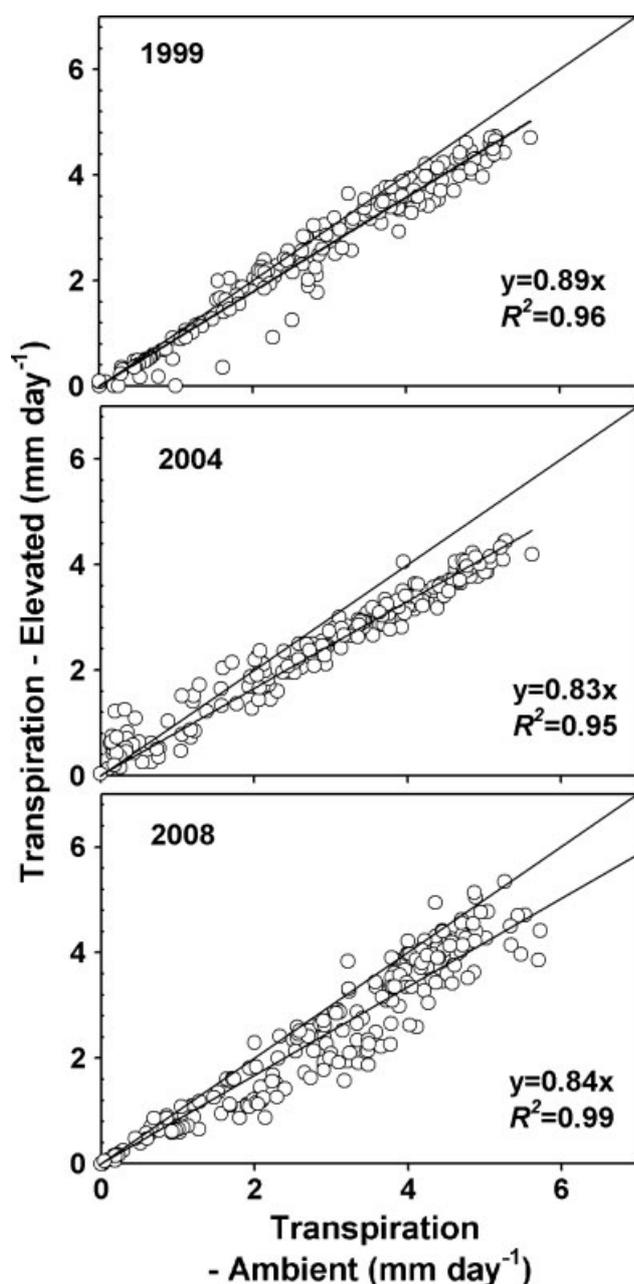


Figure 2. Measured canopy transpiration of sweetgum forest plantation FACE plots exposed to ambient or elevated atmospheric CO₂ across multiple years. Values below the solid 1:1 line represent greater transpiration in aCO₂ plots than in eCO₂ plots.

leaves and the atmosphere. Projected increases in air temperature will further increase VPDs. These feedback processes could increase transpiration and reduce water use efficiency (as grams of C uptake per gram of H₂O release), although under persistent drought and heat, stomatal conductance and stand water use slowly decline. In addition, there is an evidence of much greater reduction in water use in eCO₂ plots at ORNL FACE during extreme heat and drought events, especially for dominant trees whose measured sap flow declined by 60% relative to aCO₂ trees (Warren *et al.*, In review). Under such extreme events, the Biome-BGC model used in this study was not able to simulate measured values

of transpiration (overestimation; data not shown), which necessitates further model refinement and sensitivity to extreme climate conditions.

Water use through trees is further regulated by soil–root–leaf conductances associated with the characteristic forest structures—root deployment, xylem anatomy, tree height, branching patterns, and leaf area (Waring and Running, 1998). These structural features can change during stand development and can be altered by eCO₂, so it is important that assessments of the effects of eCO₂ on forest water use recognize the importance of stand structure, including its plasticity and temporal dynamics. Across the FACE sites compiled here, stage of stand development appeared to have the greatest influence on the response of canopy transpiration to eCO₂, where eCO₂ increased LAI and stand water use in the young rapidly growing plantations, while eCO₂ resulted in little change to LAI and substantial reductions in stand water use in the older, nutrient-limited stands.

As trees age and grow taller, structural and physiological changes can occur that affect water use. Stomatal conductance, photosynthesis, specific leaf area, and leaf-specific hydraulic conductance often are lower in taller trees, and hydraulic limitations can increase with tree height (Ryan *et al.*, 2006; Domec *et al.*, 2008). The C : N ratio of trees often increases during stand development as wood volume increases and labile N is incrementally sequestered into longer-lived pools (e.g. wood), which can reduce productivity and leaf area (Ryan *et al.*, 1997; Johnson, 2006). These factors can lead to a decline in overstorey transpiration during stand development, but a decline in total ecosystem evaporation may be offset by enhanced evapotranspiration from the soil and understorey vegetation (Delzon and Loustau, 2005). At the ORNL FACE site, there was little evidence for enhanced understorey LAI over the course of the study across treatments; however, there was an increase in the woody biomass in eCO₂ plots, which could change soil–plant evapotranspiration due to altered understorey vertical structure (Souza *et al.*, 2010).

LAI and canopy development

LAI increases rapidly as tree seedlings are established on a site until crown closure occurs, after which LAI peaks and may slowly decline. The time required to attain peak LAI during stand development depends on the availability of environmental resources and stand density. In the ORNL sweetgum plantation, LAI had already peaked when the CO₂ treatments were initiated 10 years after plantation establishment. eCO₂ can accelerate canopy development of young trees prior to canopy closure and thereby alter other processes, including water use, that depend on leaf area. Indeed, eCO₂-stimulated canopy development and LAI at the two young rapidly growing stands at Aspen-FACE and POP/EuroFACE, suggesting that the resources other than CO₂ were not limiting, and resulted in greater stand water use in eCO₂ plots. However, such observations are confined to young stands

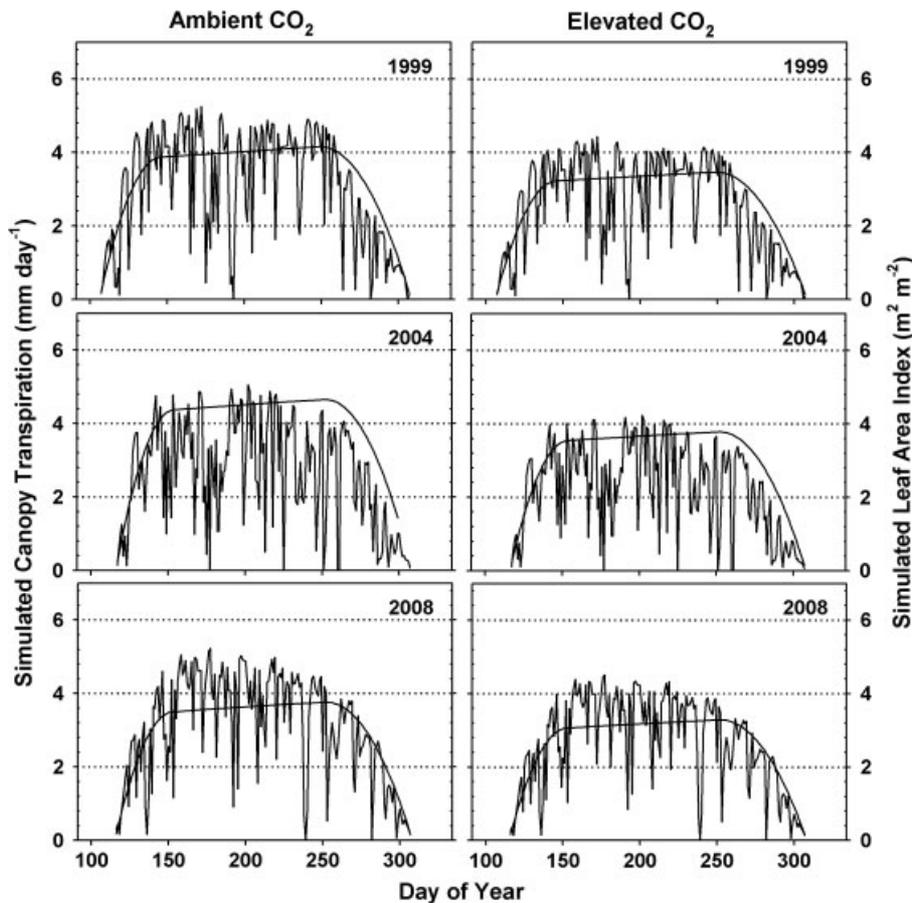


Figure 3. Simulated daily canopy transpiration in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO₂ across multiple years based on an ecosystem process model (Biome-BGC), and seasonal patterns of stimulated leaf area index (LAI) (smooth lines).

and are not overly informative in terms of water use by fully developed forest stands (Norby *et al.*, 1999).

Even with a closed canopy, the ORNL sweetgum trees displayed large inter-annual variation in LAI, which was differentially affected by the CO₂ treatments. Year-to-year variation in LAI of CO₂-enriched plots may increase sensitivity to other site resources, suggesting that the eCO₂ may create transient imbalances in resources or push the stand towards thresholds in resource availability. Recent evidence from the ORNL site does indeed reveal reduced eCO₂ stimulation of NPP through time, attributable to reduced soil N availability that is linked to enhanced N sequestration in NPP biomass and soil pools (Norby *et al.*, 2010). Despite transient or persistent shifts in eCO₂:aCO₂ of NPP or LAI, there has not been a substantial change in the E:A transpiration rates (0.84–0.90), which is likely owing to the plasticity of stomatal response.

Roots and soil water extraction

Woody ecosystems exposed to the eCO₂ often increase root production and root standing crop (Table I) and shift root distribution deeper into the soil profile (Iversen, 2010), both processes that could alter water extraction dynamics. Access to deep water is important in many water-limited ecosystems, but the relationship between fine-root distribution and water uptake is not clear

and remains an important need for models (Jackson *et al.*, 2000). Root distribution was not well correlated to patterns of water extraction in several coniferous forests under drying conditions, as a minor fraction of roots at deeper depths seasonally provided the major fraction of water uptake (Warren *et al.*, 2005). Thus, knowledge of vertical patterns of water extraction across the season may be more important than knowledge of root distribution.

Quantification of water content in only the upper soil (~0–20 cm) at the five forest FACE studies thus may not necessarily reflect root water extraction dynamics as affected by CO₂ treatments, and may further be confounded by spatial variation in water content due to lateral water movement across the landscape (Schäfer *et al.*, 2002). Under moderate drought, there was reduced sap flow in mature deciduous trees exposed to eCO₂, which led to a slower decline in upper soil moisture than in aCO₂ plots; however, treatment differences in water content at 10 cm were not apparent during a more severe drought (Leuzinger and Körner, 2007), suggesting differences in deeper root water extraction patterns. In addition, eCO₂ significantly increased tree growth and sap flow in the mixed *Populus tremuloides*, *Betula papyrifera*, and *Acer saccharum* Aspen-FACE study, yet there was no decline, or even an increase in upper soil water content (Uddling *et al.*, 2008).

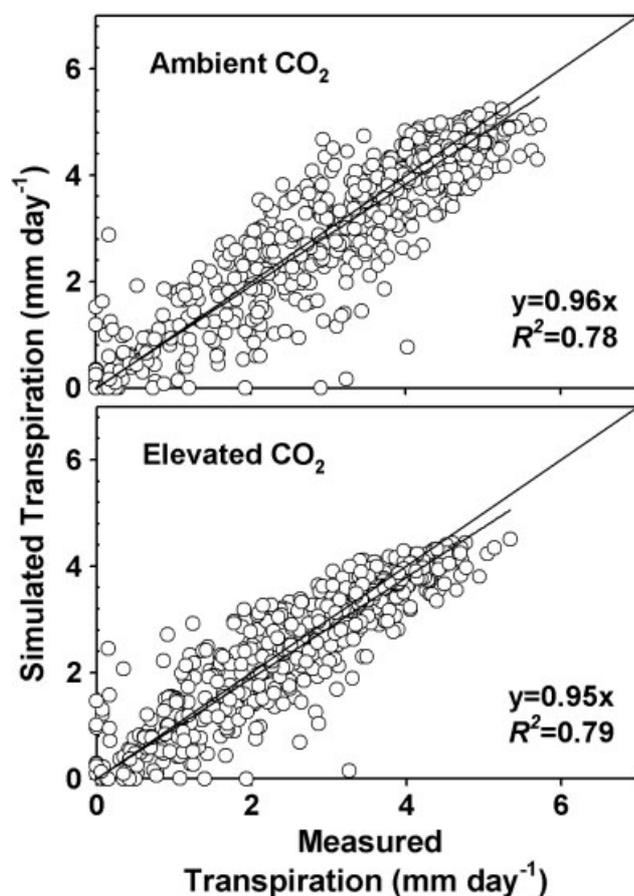


Figure 4. Canopy transpiration from ambient and elevated CO₂ plots through time as scaled from sap flow analysis (measured) and from parameterized modeling using Biome-BGC (simulated).

SOM and soil water availability

Soil water availability might also be increased by eCO₂ treatments due to the increased SOM or surface litter inputs that reduce evaporation (Schäfer *et al.*, 2002; Uddling *et al.*, 2008). There is an evidence for increased litter build-up in the forest floor under eCO₂ at Duke FACE (Lichter *et al.*, 2005) and POP/EuroFACE (Hoosbeek and Scarascia-Mugnozza, 2009), and there is evidence for increased SOM under eCO₂ in the uppermost soil layer (0–5 cm) at ORNL FACE (Jastrow *et al.*, 2005). Analyses of deeper layers (e.g. 0–15 cm) have not been able to show significant increases in SOM (Jastrow *et al.*, 2005; Lichter *et al.*, 2005), despite measured increases in root production and turnover at depth at these two sites (Iversen *et al.*, 2008; Pritchard *et al.*, 2008). If at a longer timescale, eCO₂ treatments resulted in a doubling of SOM in upper soil at the ORNL FACE, Duke FACE, or Aspen-FACE sites (e.g. 1.5–3.0% SOM), field capacity (water content at -0.033 MPa) could potentially increase by up to 12% based on equations in Rawls *et al.* (2003) using upper soil C and textural data (Dickson *et al.*, 2000; Jastrow *et al.*, 2005; D. Todd, unpublished; Oh and Richter, 2005). At the ORNL FACE site, eCO₂ has increased SOM in the 0–5 cm soil layer by $\sim 10\%$ over five years compared with aCO₂ (Jastrow *et al.*, 2005), correlating to $\sim 1\%$ increase in modelled

field capacity for this site (i.e. 0.341 and 0.345 m³ m⁻³, for aCO₂ and eCO₂). As SOM accumulation is relatively slow and declines with depth in the soil profile, the resulting impact on soil water retention during the course of these FACE studies is ecologically minor for forest species that rely on water extraction throughout the soil profile, although, across multi-decadal timescales, eCO₂-enhanced litter production may accelerate soil C accrual and reduce surface soil evaporation, and thus improve inherent water retention as forest soils develop, especially for previously cultivated and degraded soils low in SOM.

Simulations and model performance

Simulated LAI was up to 20% (aCO₂) to 45% (eCO₂) lower than the measured values and quite stable through time. Measured LAI was dramatically reduced during two extreme years (2004 windstorm, 2008 post-drought); however, simulated LAI was not able to model these events, resulting in simulated LAI actually much closer to measured LAI in these years (within 1% aCO₂ or 5–15% eCO₂). Even though the simulations failed to accurately model seasonal or inter-annual dynamics of LAI, they were able to predict the relative magnitudes of transpiration as affected by CO₂. These results reveal both the relative importance of LAI to the model, as well as the potential for improvement in other model processes linked to transpiration. Indeed, because of the dampened peak LAI, the model is less sensitive to LAI than other process-based models (Siqueira *et al.*, 2006).

Simulated transpiration was strongly correlated to measured transpiration during the peak summer months, but overestimated in spring, and either underestimated (aCO₂) or overestimated (eCO₂) in autumn. These deviations could have significant impacts on seasonal patterns of water availability and net carbon uptake by initially accelerating seasonal water use that could induce seasonal drought earlier than might be expected. For the eCO₂ stands, this effect would be increased in autumn, potentially offsetting the benefits of eCO₂-reduced transpiration to net water balance. Failure to properly simulate timing of leaf out in the spring and senescence in the fall, and a lack of sensitivity to stress events can have a large impact on seasonal water use. Future studies should focus on these areas of uncertainty.

The C:N ratios, C and N allocation parameters, and specific leaf area were not dynamic parameters in the model, therefore the general mechanisms and dependencies causing shifts in these parameters over time are still not clear. Although the trends in these parameters appear linear over the course of this 12-year observation period, a continuation of the same trends into older developmental stages cannot be anticipated. Previous studies applying this model across forest chronosequences have concluded that the introduction of explicit age-class dynamics would improve model performance (Law *et al.*, 2001, 2003),

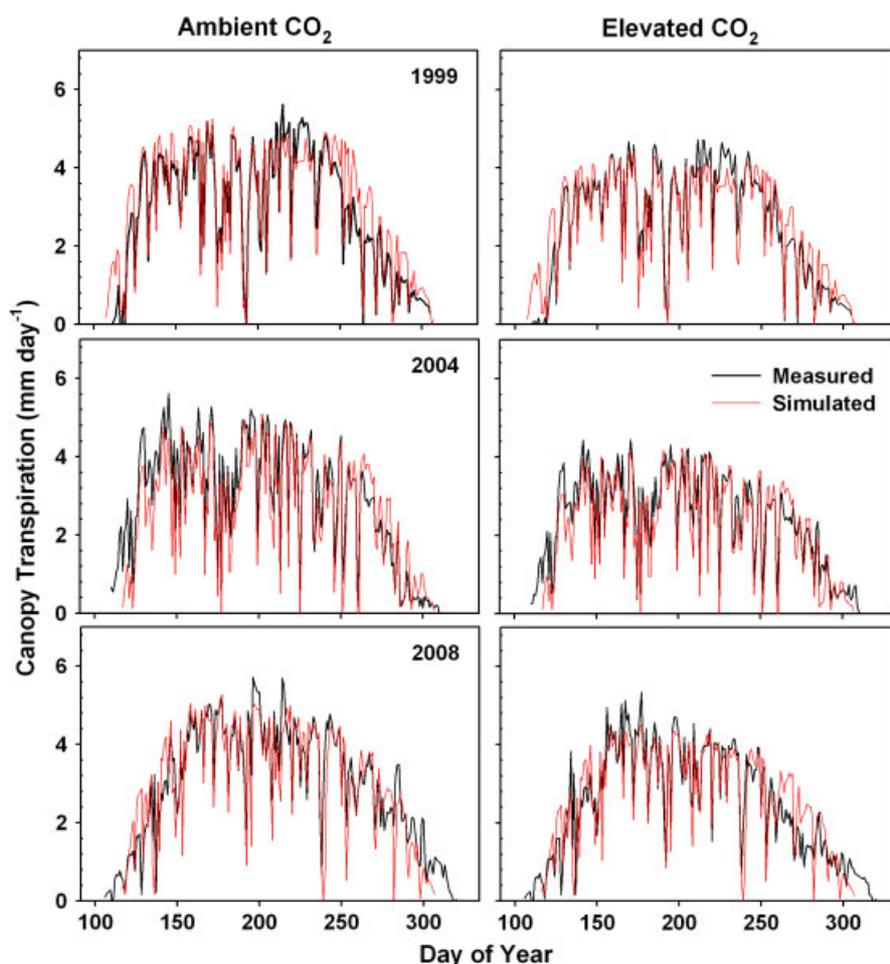


Figure 5. Comparison between measured and simulated daily canopy transpiration in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO₂ across multiple years (1999, 2004, and 2008).

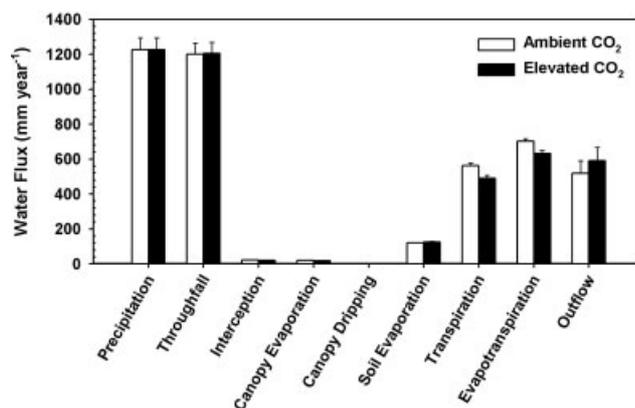


Figure 6. Simulated annual water flux components for the sweetgum forest plantation FACE plots exposed to ambient (a) or elevated (e) atmospheric CO₂. Values represent mean ecosystem response from 1998 to 2008 (\pm s. e. across years), based on parameterization to 1999 measured values and a 10 000 year spin-up cycle.

and our results support that finding. To assess the water budget during the ORNL FACE experiment, it was most feasible to use mean values for the measured ecophysiological parameters for two reasons. First, we were only interested in the 12 years of the experiment—a relatively short application time for the ecosystem model Biome-BGC. Second, as long as LAI remains at a reasonably

high level, the water budget is not strongly influenced by shifts in these ecophysiological parameters.

In this regard, it should also be mentioned that additional allocation of biomass to the root system as stipulated by model parameters, and as observed for the eCO₂ treatment, does not provide any benefit for the simulated forest as neither nitrogen availability nor water uptake depend on the root biomass. Biome-BGC does not explicitly include root distribution within the vertical soil profile or rooting depth. Rather, the model uses the user-parameterized effective soil depth to describe total water availability from the system. The model logic is based on the assumption that tree roots will exploit the entire soil profile as necessary to provide a minimal water supply during dry periods. Maximum rooting depth is not assessed in many studies, but can be effectively modelled on the basis of potential evapotranspiration and knowledge of soil water distribution (Schenk, 2008). However, it should be kept in mind that modelling soil and rooting depth may be limited to individual species. In a mixed Douglas-fir–western hemlock forest, there is species specificity of the depth of active rooting and water extraction (Meinzer *et al.*, 2007) that would complicate model assumptions.

CONCLUSIONS

The measurement, modelling, and synthesis activities conducted in this study reveal that several important aspects of site water balance and ecosystem function are likely to be impacted by rising atmospheric CO₂ in the coming decades. Ecohydrological implications of ecosystem response to rising CO₂ will be site specific and temporally dynamic, dependent on stand development and successional state. In the case of temperate deciduous forests, and barring effects of eCO₂ on LAI, reductions in canopy transpiration and stand water use due to direct effects of CO₂ on stomatal conductance will be reflected in increased soil water content and potential water yield. Our results support the expectation that large-scale regional soil and climate limitations to eCO₂ enhancement of forest productivity may lead to increased surface runoff directly through reduction in stomatal conductance (Betts *et al.*, 2007). Increased availability of water within a mixed species forest will have consequences for how individual trees and tree species respond to low soil water potentials during periods of water-deficit stress and for patterns of plant–plant competition for available water resources. To date, such observations have been beyond the scope of our experiments, although next-generation gap or biogeography models could be used to explore possible implications. Future simulations might also be extended to shifts in temperature and precipitation associated with climate change, including extreme events that are projected to increase in frequency. However, empirical multivariate studies necessary for validating and parameterizing more complex simulations (Luo *et al.*, 2008) are largely lacking, and may be difficult to assess due to interactive responses.

ACKNOWLEDGEMENTS

Editorial assistance was provided by Tara A. Hall. Data compilation and literature surveys were provided by Elizabeth C. Storey. This research was funded by the US Department of Energy, Office of Science, Biological and Environmental Research. ORNL is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-00OR22725.

REFERENCES

- Bader M, Hiltbrunner E, Körner C. 2009. Fine root responses of mature deciduous forest trees to free air carbon dioxide enrichment (FACE). *Functional Ecology* **23**: 913–921.
- Barrett DJ, Hatton TJ, Ash JE, Ball MC. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rain-forest and Eucalyptus forest species of south-eastern Australia. *Plant Cell and Environment* **18**: 463–469.
- Betts RA, Boucher O, Collins M, Cox PM, Falloon PD, Gedney N, Hemming DL, Huntingford C, Jones CD, Sexton D, Webb MJ. 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* **448**: 1037–1041.
- Cech PG, Pepin S, Körner C. 2003. Elevated CO₂ reduces sap flux in mature deciduous forest trees. *Oecologia* **137**: 258–268.
- Chahine MT. 1992. The hydrological cycle and its influence on climate. *Nature* **359**: 373–380.
- Clapp RB, Hornberger GM. 1978. Empirical equations for some soil hydraulic properties. *Water Resources Research* **14**: 601–604.
- Cosby BJ, Hornberger GM, Clapp RB, Ginn TR. 1984. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resources Research* **20**: 682–690.
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox P, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C. 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**: 357–373.
- de Pury DGG, Farquhar GD. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell and Environment* **20**: 537–557.
- Delzon S, Loustau D. 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agricultural and Forest Meteorology* **129**: 105–119.
- Dickson RE, Lewin KF, Isebrands JG, Coleman MD, Heilman WE, Riemenschneider DE, Sober J, Host GE, Zak DR, Hendrey GR, Pregitzer KS, Karnosky DF. 2000. *Forest atmosphere carbon transfer and storage (FACTS-II) the aspen Free-air CO₂ and O₃ Enrichment (FACE) project: an overview*. Gen Tech. Rep. NC-214. USDA Forest Service, North Central Research Station: St. Paul, MN; 68.
- Domec J-C, Lachenbruch BL, Meinzer FC, Woodruff D, Warren JM, McCulloh KA. 2008. Maximum height in a conifer is associated with conflicting requirements for xylem design. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 12069–12074.
- Ellsworth DS. 1999. CO₂ enrichment in a maturing pine forest: are CO₂ exchange and water status in the canopy affected? *Plant Cell and Environment* **22**: 461–472.
- Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey GR. 1995. Leaf and canopy responses to elevated CO₂ in a pine forest under free-air CO₂ enrichment. *Oecologia* **104**: 139–146.
- Ewers BE, Gower ST, Bond-Lamberty B, Wang CK. 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell and Environment* **28**: 660–678.
- Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch S. 2004. Terrestrial vegetation and water balance-hydrological evaluation of a dynamic global vegetation model. *Journal of Hydrology* **286**: 249–270.
- Granier A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* **3**: 309–319.
- Granier A, Reichstein M, Breda N, *et al.* 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* **143**: 123–145.
- Gunderson GA, Sholtis JD, Wullschlegel SD, Tissue DT, Hanson PJ, Norby RJ. 2002. Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO₂ enrichment. *Plant Cell and Environment* **25**: 379–393.
- Hanson PJ, Wullschlegel SD, Norby RJ, Tschaplinski TJ, Gunderson CA. 2005. Importance of changing CO₂, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. *Global Change Biology* **11**: 1402–1423.
- Hendrey GR, Ellsworth DS, Lewin KF, Nagy J. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* **5**: 293–309.
- Hoosbeek MR, Scarascia-Mugnozza GE. 2009. Increased litter build up and soil organic matter stabilization in a poplar plantation after six years of atmospheric CO₂ enrichment (FACE): Final results of POP-EUROFACE compared to other forest FACE experiments. *Ecosystems* **12**: 220–239.
- Iversen CM. 2010. Minireview—Digging deeper: fine-root responses to rising atmospheric CO₂ concentration in forested ecosystems. *New Phytologist* **186**: 346–357.
- Iversen CM, Ledford J, Norby RJ. 2008. CO₂ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist* **179**: 837–847.
- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW. 2001. Water in a changing world. *Ecological Applications* **11**: 1027–1045.
- Jackson RB, Schenk HJ, Jobbagy EG, Canadell J, Colello GD, Dickinson RE, Field CB, Friedlingstein P, Heimann M, Hibbard K, Kicklighter DW, Kleidon A, Neilson RP, Parton WJ, Sala OE, Sykes MT. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* **10**: 470–483.

- Jastrow JD, Miller RM, Matamala R, Norby RJ, Boutton TW, Rice CW, Owensby CE. 2005. Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology* **11**: 2057–2064.
- Johnson DW. 2006. Progressive N limitation in forests: Review and implications for long-term responses to elevated CO₂. *Ecology* **87**: 64–75.
- Keel SG, Pepin S, Leuzinger S, Körner C. 2007. Stomatal conductance in mature deciduous forest trees exposed to elevated CO₂. *Trees* **21**: 151–159.
- King JS, Kubiske ME, Pregitzer KS, Hendrey GR, McDonald EP, Giardina CP, Quinn VS, Karnosky DF. 2005. Tropospheric O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *New Phytologist* **168**: 623–636.
- Körner C. 1995. Leaf diffusive conductances in the major vegetation types of the globe. In *Ecophysiology of Photosynthesis*, Schulze E-D, Caldwell MM (eds). Springer-Verlag: New York; 463–490.
- Kuehn GD, McFadden BA. 1969. Ribulose 1,5-bisphosphate carboxylase from *Hydrogenomonas eutropha* and *H. facilis*. II. Molecular weight, subunits, composition, and sulfhydryl groups. *Biochem. J.* **8**: 2403–2408.
- Law BE, Sun OJ, Campbell J, Van Tuyl S, Thornton PE. 2003. Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology* **9**: 510–514.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology* **7**: 755–777.
- Law BE, Waring RH, Anthoni PM, Aber JD. 2000. Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* **6**: 155–168.
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Alistair R, Long SP, Ort DR. 2009. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: size important lessons from FACE. *Journal of Experimental Botany* **60**: 2859–2876.
- Leuzinger S, Körner C. 2007. Water savings in mature deciduous forest trees under elevated CO₂. *Global Change Biology* **13**: 2498–2508.
- Leuzinger S, Körner C. 2010. Rainfall distribution is the main driver of runoff under future CO₂-concentration in a temperate deciduous forest. *Global Change Biology* **16**: 246–254.
- Leuzinger S, Zotz G, Asshoff R, Körner C. 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiology* **25**: 641–650.
- Liberloo M, Dillen SY, Calfapietra C, Marinari S, Luo ZB, de Angelis P, Ceulemans R. 2005. Elevated CO₂ concentration, fertilization and their interaction: growth stimulation in a short-rotation poplar copice (EUROFACE). *Tree Physiology* **25**: 179–189.
- Lichter J, Barron S, Finzi A, Irving K, Roberts M, Stemmler E, Schlesinger W. 2005. Soil carbon sequestration and turnover in a pine forest after six years of atmospheric CO₂ enrichment. *Ecology* **86**: 1835–1847.
- Loaiciga HA, Valdes JB, Vogel R, Garvey J, Schwarz H. 1996. Global warming and the hydrologic cycle. *Journal of Hydrology* **174**: 83–127.
- Lukac M, Calfapietra C, Godbold DL. 2003. Production, turnover and mycorrhizal colonization of root systems of three *Populus* species grown under elevated CO₂ (POPFACE). *Global Change Biology* **9**: 838–848.
- Luo Y, Gerten D, le Maire G, Parton WJ, Weng E, Zhou X, Keough C, Beier C, Ciais P, Cramer W, Dukes JS, Emmett B, Hanson PJ, Knapp A, Linder S, Nestad D, Rustad L. 2008. Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* **14**: 1986–1999.
- McCarthy HR, Oren R, Finzi A, Ellsworth DS, Kim H-S, Johnsen K, Millar B. 2007. Temporal dynamics and spatial variability in the enhancement of canopy leaf area under elevated atmospheric CO₂. *Global Change Biology* **13**: 2479–2497.
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C. 2007. Global Climate Projections. In *Climate Change 2007: The Physical Science Basis Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds). Cambridge University Press: Cambridge, New York.
- Meinzer FC, Warren JM, Brooks JR. 2007. Species-specific partitioning of soil water resources in an old-growth Douglas-fir/western hemlock forest. *Tree Physiology* **27**: 871–880.
- Newman BD, Wilcox BP, Archer SR, Breshears DD, Dahm CN, Duffy CJ, McDowell NG, Phillips FM, Scanlon BR, Vivoni ER. 2006. Ecohydrology for water-limited environments: a scientific vision. *Water Resources Research* **42**: DOI: 10.1029/2005WR004141.
- Noormets A, Söber A, Pell EJ, Dickson RE, Podila GK, Söber J, Isebrands JG, Karnosky DF. 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO₂ and/or O₃. *Plant Cell and Environment* **24**: 327–336.
- Norby RJ, Tharp ML. 2008. ORNL FACE Leaf Area Index LAI Data. Carbon Dioxide Information Analysis Center <http://cdiac.ornl.gov>, U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN.
- Norby RJ, DeLucia EH, Gielen B, *et al.* 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 18052–18056.
- Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RT, Cheng W, Wullschlegler SD, Gunderson CA, Edwards NT, Johnson DW. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* **12**: 1261–1266.
- Norby RJ, Kobayashi K, Kimball BA. 2001. Commentary—Rising CO₂—future ecosystems. *New Phytologist* **150**: 215–221.
- Norby RJ, Sholtis JD, Gunderson CA, Jawdy SS. 2003. Leaf dynamics of a deciduous forest canopy: no response to elevated CO₂. *Oecologia* **136**: 574–584.
- Norby R, Warren J, Iversen C, Garten C, Medlyn B, McMurtrie R. 2010. CO₂ enhancement of forest productivity constrained by limited nitrogen availability *Proceedings of the National Academy of Sciences (in press)*.
- Norby RJ, Wullschlegler SD, Gunderson CA, Johnson DW, Ceulemans R. 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell and Environment* **22**: 683–714.
- Oh N-H, Richter DD. 2005. Elemental translocation and loss from three highly weathered soil—bedrock profiles in the southeastern United States. *Geoderma* **126**: 5–25.
- Pietsch SA, Hasenauer H. 2006. Evaluating the self-initialization procedure of large scale ecosystem models. *Global Change Biology* **12**: 1658–1669.
- Pregitzer KS, Burton AJ, King JS, Zak D. 2008. Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO₂ and tropospheric O₃. *New Phytologist* **180**: 153–161.
- Pritchard SG, Strand AE, McCormack ML, Davis MA, Finzi AC, Jackson RB, Matamala R, Rogers HH, Oren R. 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.
- Rawls WJ, Pachepsky YA, Ritchie JC, Sobecki TM, Bloodworth H. 2003. Effect of soil organic carbon on soil water retention. *Geoderma* **116**: 61–76.
- Riggs JS, Tharp ML, Norby RJ. 2009. ORNL FACE CO₂ and Weather Data. Carbon Dioxide Information Analysis Center (<http://cdiac.ornl.gov>), U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* **27**: 213–262.
- Ryan MG, Phillips N, Bond BJ. 2006. The hydraulic limitation hypothesis revisited. *Plant Cell and Environment* **29**: 367–381.
- Saxton KE, Rawls WJ, Romberger JS, Papendick RI. 1986. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* **50**: 1031–1036.
- Schäfer KVR, Oren R, Lai C, Katul GG. 2002. Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO₂ concentration. *Global Change Biology* **8**: 895–911.
- Schenk HK. 2008. The shallowest possible water extraction profile: a null model for global root distributions. *Vadose Zone Journal* **7**: 1119–1124.
- Sholtis JD, Gunderson CA, Norby RJ, Tissue DT. 2004. Persistent stimulation of photosynthesis by elevated CO₂ in a sweetgum (*Liquidambar styraciflua* L.) forest stand. *New Phytologist* **162**: 343–354.
- Siqueira MB, Katul GG, Sampson DA, Stoy PC, Juang J-Y, McCarthy HR, Oren R. 2006. Multiscale model intercomparisons of CO₂ and H₂O exchange rates in a maturing southeastern US pine forest. *Global Change Biology* **12**: 1189–1207.

- Souza L, Belote RT, Kardol P, Weltzin JF, Norby RJ. 2010. CO₂ enrichment accelerates successional development of an understory plant community. *Journal of Plant Ecology-UK* **3**: 33–39.
- Sperry JS, Adler FR, Campbell GS, Comstock JP. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**: 347–359.
- Thornton PE, Law BE, Gholz HL, Clark KL, Falge E, Ellsworth DS, Goldstein AH, Monson RK, Hollinger D, Falk M, Chen J, Sparks JP. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology* **113**: 185–222.
- Thornton PE, Rosenbloom NA. 2005. Ecosystem model spin-up: estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecological Modelling* **189**: 25–48.
- Tricker PJ, Pecchiari M, Bunn SM, Vaccari FP, Peressotti A, Miglietta F, Taylor G. 2009. Water use of a bioenergy plantation increase in a future high CO₂ world. *Biomass & Bioenergy* **33**: 200–208.
- Tricker PJ, Trewin H, Kull O, Clarkson GJJ, Eensalu E, Tallis MJ, Colella A, Doncaster CP, Sabatti M, Taylor G. 2005. Stomatal conductance and not stomatal density determines the long-term reduction in leaf transpiration for poplar in elevated CO₂. *Global Change Biology* **143**: 652–660.
- Uddling J, Teclaw RM, Kubiske ME, Pregitzer KS, Ellsworth DS. 2008. Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **28**: 1231–1243.
- Uddling J, Teclaw RM, Pregitzer KS, Ellsworth DS. 2009. Leaf and canopy conductance in aspen and aspen-birch forests under free air enrichment of carbon dioxide and ozone. *Tree Physiology* **29**: 1367–1380.
- Waring RH, Running SW. 1998. *Forest Ecosystems Analysis at Multiple Scales*. Academic Press: San Diego, CA.
- Warren JM, Meinzer FC, Brooks JR, Domec JC. 2005. Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Agricultural and Forest Meteorology* **130**: 39–58.
- Warren JM, Norby RJ, Wullschleger SD. In review. Elevated CO₂ enhances leaf senescence during extreme heat and drought in a temperate forest. *Tree Physiology*.
- White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology* **42**: 139–145.
- White MA, Thornton PE, Running SW, Nemani RR. 2000. *Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls*. Earth Interactions Paper 4–003.
- Wilson KB, Hanson PJ, Mulholland PJ, Baldocchi DD, Wullschleger SD. 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance, and catchment in water balance. *Agricultural and Forest Meteorology* **106**: 153–168.
- Woodrow IE, Berry JA. 1988. Enzymatic regulation of photosynthetic CO₂ fixation in C3 plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**: 533–594.
- Wullschleger SD. 1993. Biochemical limitations to carbon assimilation in C3 plants—A retrospective analysis of the A/Ci curves from 109 species. *Journal of Experimental Botany* **44**: 907–920.
- Wullschleger SD, Gunderson CA, Hanson PJ, Wilson KB, Norby RJ. 2002b. Sensitivity of stomatal and canopy conductance to elevated CO₂ concentration—interacting variables and perspectives of scale. *New Phytologist* **153**: 485–496.
- Wullschleger SD, Norby RJ. 2001. Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO₂ enrichment (FACE). *New Phytologist* **150**: 489–498.
- Wullschleger SD, Norby RJ, Hendrix DL. 1992. Carbon exchange rates, chlorophyll concentration, and carbohydrate status of two forest tree species to carbon dioxide enrichment. *Tree Physiology* **10**: 21–31.
- Wullschleger SD, Tschaplinski TJ, Norby RJ. 2002a. Plant water relations at elevated CO₂—implications for water-limited environments. *Plant Cell and Environment* **25**: 319–331.

APPENDIX III-II

For study III (Appendix III; Warren et al., 2011b), we could rely on a particularly high number of ecophysiological and productivity measurements from the 12-year experiment. This facilitated a site, species and CO₂-treatment specific parameterisation of Biome-BGC. In the following, more details are given on those ecophysiological parameters which are treated with less detail in Warren et al. (2011b).

Transfer growth period and litter fall period: The transfer growth period (TGP) defines the time in spring when stored C is deployed for leaf flush and early season plant growth. The litter fall period (LFP) defines the time in autumn when the leaves are shed. Both are expressed as a fraction of the growing season length. The TGP and LFP fractions were estimated from all-season LAI curves for aCO₂ and eCO₂, available for all years of the experiment. A TGP fraction of 0.2 and a LFP fraction of 0.3 gave the best agreement between simulated and measured seasonal LAI development.

Carbon and nitrogen allocation The allometric parameters that relate C distribution among fine and coarse roots, wood and leaves were derived from measurements of annual growth for the different plant compartments for the years 1998 – 2007 (Iversen et al., 2008; Norby et al., 2004, 2002, 2001). Statistically significant trends over time were apparent for the ratios 'new coarse root C to new wood C' and 'new wood C to new leaf C' for both treatments. Since Biome-BGC does not allow changing parameters over stand development, the average over all years was used.

C/N ratios: Carbon to nitrogen ratios for all plant compartments are used in Biome-BGC to determine the maintenance respiration (a function of the N-content) and the maximum rate of carboxylation (V_{cmax}) of the leaves. Biomass and N-content of the relevant plant compartments had been measured annually (Norby and Tharp, 2008; Norby et al., 2008). From these data and the known C-fractions (Norby et al., 2002) the C/N ratios could be derived. The C/N showed a positive trend over time for most compartments, but again, the mean over the observation period had to be used.

Specific leaf area: The canopy average specific leaf area (SLA) was derived from data on canopy average leaf mass per area (LMA; Norby and Iversen, 2006). The LMA was multiplied with the C-content of the leaves, then the inverse was calculated to get the SLA. Although a negative trend over the years was apparent for both treatments, once more, the mean over the whole observation period had to be used. In addition, the SLA ratio of shaded to sunlit leaves was needed. It was calculated from LMA measured in one meter steps over the whole canopy depth for the years 1999 and 2009. The LMA at every canopy depth was weighted by the measured LAI. The upper two meters in the canopy were used to get the average sunlit LMA, the canopy parts below were used to derive the average shaded LMA. The LMA values were converted into the SLA as described above.

APPENDIX IV

Pötzelsberger, E., Wolfslehner, B., Hasenauer, H., 2015. Climate change impacts on key forest functions of the Vienna Woods. *Eur. J. For. Res.* doi: 10.1007/s10342-015-0866-2

Climate change impacts on key forest functions of the Vienna Woods

Elisabeth Pötzelsberger · Bernhard Wolfslehner ·
Hubert Hasenauer

Received: 14 February 2014 / Revised: 22 December 2014 / Accepted: 21 January 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract A temperature increase higher than the global mean is likely for Central Europe until the end of the century. Historic climate records reveal that the temperature in eastern Austria has already increased by about 2 °C over the last 50 years. We investigated the responses of ecophysiological and productivity indicators to climate change of the Vienna Woods, the neighbouring forests of the Austrian capital, to assess potential impacts on forest functioning. In this impact analysis, we used the biogeochemical mechanistic model Biome-BGC and ran it with 50 years of historic climate data and regional climate change projections based on IPCC emission scenarios A1B and B1 until 2100. We projected sustained productivity until the end of the twenty-first century. Lowered soil water potentials, however, seem to limit a productivity increase, especially in the low elevation areas, while the canopy leaf area, annual soil water outflow and annual mean water use efficiency are projected to remain constant or increase. We conclude that the forests in the greenbelt of Vienna are not severely prone to negative functional climate change effects, and therefore, key forest functions concerning welfare and recreation can be maintained in the Vienna Woods.

Keywords Beech forests · Climate change · Forest functions · Vienna Woods

Introduction

The role of forests in and around densely populated areas is of increasing interest since they cover a broad range of environmental, social and economic issues (Konijnendijk et al. 2005; Carreiro et al. 2008; Konijnendijk 2008; Young 2010). Functioning forests secure the traditional use of forests for timber production as well as the provision of a variety of important non-timber forest products and services, such as welfare and recreation (Oleyar et al. 2008; Dobbs et al. 2011). Climate change impact studies deal with potential latitudinal (Woodall et al. 2010) and altitudinal shifts in tree species (Peñuelas et al. 2007), increasing biotic and abiotic disturbances (Dukes et al. 2009; Seidl et al. 2014), socioeconomic impacts (e.g. creation of new, 'green' jobs, Renner et al. 2008), climate change adaptation (Lindner et al. 2010) and mitigation options (Millar et al. 2007; Zheng et al. 2013) and climate change impact on ecophysiology and productivity (Hyvönen et al. 2006; Luo et al. 2008). Latter will impact forest ecosystem functioning with possible consequences on welfare and recreation, for example, due to the stabilising effects of forests for the urban microclimate (Peters and McFadden 2010) or role of forests in the water supply (Furniss et al. 2010).

In the present study, we are interested in the climate change impact on ecophysiology- and productivity-based key forest functions of the famous 'Wienerwald' or the 'Vienna Woods' that borders the Austrian capital. This European beech (*Fagus sylvatica* L.) dominated forest is located in the transition zone between the eastern edge of

Communicated by Martin Moog.

E. Pötzelsberger (✉) · B. Wolfslehner · H. Hasenauer
Institute of Silviculture, University of Natural Resources and
Life Sciences, Vienna, Peter-Jordanstr. 82, 1190 Vienna, Austria
e-mail: elisabeth.potzelsberger@boku.ac.at

B. Wolfslehner
European Forest Institute, Central-East European Regional
Office (EFICEEC), Vienna, Austria

the Alps and the Pannonic lowlands and includes a UNESCO biosphere reserve. The forest provides important ecosystem services to Vienna's urban population, such as recreation, welfare, fresh air, climate, fresh water, protection against soil erosion and timber. The forest is explicitly managed to attain these goals (Foet 2010; Albrecht 2011).

European beech is one of the most dominant tree species in Europe with a wide distribution in Central and Western Europe. In the last decades, beech forests have experienced increased growth rates in Central Europe, mostly attributed to increased nitrogen deposition, higher temperatures and CO₂ levels (Pretzsch et al. 2014). European beech avoids regions with long, very cold winters or long dry periods in summer and is often said to require a minimum annual precipitation of 600 mm (Forstreuter 2002), although the actual minimum will depend on the distribution of precipitation among the seasons and on the soil conditions (Ellenberg and Leuschner 2010). Due to the species' sensitivity to water supply (Granier et al. 2007), the future of beech at a southern or lower elevation distribution limit is uncertain under expected climate change (Mátyás et al. 2010; Hlásny et al. 2011; Tegel et al. 2013).

For this study, we used biogeochemical mechanistic modelling to assess potential climate change-driven impacts on forest functioning (not including storm or biotic disturbances) using the process-based ecosystem model Biome-BGC as a diagnostic tool. We employed 50 years of local historic climate data, four regional climate change scenarios for the horizon 2100 and corresponding atmospheric CO₂ concentrations to drive the model. The scenarios are based on the IPCC emission scenarios A1B and B1, and both are used with and without an additional precipitation scenario. We were interested in (1) investigating changes of ecophysiology and productivity measures and (2) deriving indications of changes in forest functions relevant for welfare and recreation within the Vienna Woods.

Materials and methods

Study area

The study region covers the Vienna Woods, the largest broadleaf forest in Austria which lies south-west of the capital city of Vienna. The area is located at the eastern edge of the Limestone Alps and comprises non-forested areas such as agricultural land and some smaller settlements. The total study region area is about 140,000 ha within the provinces of Lower Austria and Vienna. A major part of the area (105,000 ha) is a UNESCO biosphere reserve. Elevation ranges from 140 to 1,000 m. Annual mean temperature and annual mean precipitation (mean 1960–2009) range from 5.9

to 10.6 °C and from 550 to 1,290 mm, respectively. Current nitrogen deposition rates are between 7 and 26 kg N ha⁻¹ year⁻¹ (Eastaugh et al. 2011).

The Vienna Woods cover highly productive broadleaved European beech (*F. sylvatica* L.) dominated forests that face strong recreational demands by the urban population. For many centuries, the Vienna Woods were royal hunting grounds. Wood production has become increasingly important over the last 400 years. Plans of the later nineteenth century to clear the forest and build housing were dismissed due to broad public resistance. Today, the forests are managed by the Vienna Forest Administration and the Austrian Federal Forests. Although timber production is still important, the forests are explicitly managed to address societal demands. For instance, approximately 95 % of the forest area is used for recreational purposes with around 500,000 visitors annually.

According to the European forest types (Larsson 2001), the predominant beech forests can be categorised as 5a 'lowland and submontane beech forest', where *F. sylvatica* is the dominating tree species due to its high competitiveness and often forms monospecific and monolayered forests. The lower elevations also feature oak–hornbeam (*Quercus robur* L., *Carpinus betulus* L.) forests, and a less dense downy oak (*Quercus pubescens* Willd.) forest can be found in the drier parts of the area on calcareous bedrock (Landsteiner 1990).

Figure 1 gives an overview of the forest cover in the study region with its dominating forest types (broadleaved, mixed, etc.). It also shows the 782 grid points (1 km × 1 km) within

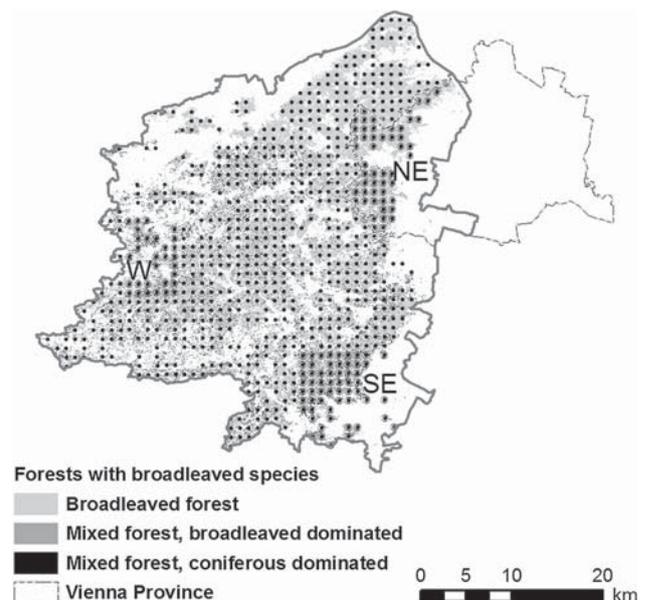


Fig. 1 Forest area with the main forest categories in the study area; the 782 forest simulation points on a 1 km × 1 km grid, and three sub-regions with simulation points in the north-east (NE), south-east (SE) and west (W)

the forest area, where the analyses were performed. Due to the predominance of beech, we treated the whole forest area as a beech forest. Climate change assessments, ecophysiology considerations and analysis of potential productivity responses are done for the forested part only. For more detailed regional analysis, we selected grid points from three sub-regions in the north-east (NE), the south-east (SE) and west (W, Fig. 1). Each sub-region is characterised by a strong elevation gradient. The NE plots comprise all simulation plots within the city of Vienna boundaries. Information on the forest cover was obtained from a GIS raster layer provided by the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW). The GIS layer is based on data of the Austrian National Forest Inventory of the period 2000–2002 and LANDSAT data from 2000 to 2003 (Koukal 2004).

Climate data

Daily weather data are key ecosystem model drivers. The climate data used for this study consisted of daily weather data using (1) historic records from the year 1960 to 2009 and (2) climate change scenarios for the years 2010–2100.

Historic climate data

The historic daily minimum and maximum temperature (T_{\min} , T_{\max}) and precipitation (Prcp) data came from climate stations provided by the Austrian Central Institute for Meteorology and Geodynamics (ZAMG). To produce daily weather data on a 1 km \times 1 km grid, we applied DAYMET (Thornton et al. 1997). DAYMET is a climate interpolation and simulation tool adapted and validated for Austria (Thornton et al. 2000; Petritsch 2002; Hasenauer et al. 2003). For the period of 1960–2009, daily T_{\min} , T_{\max} and Prcp were interpolated from 25 and 15 stations, respectively, and solar radiation (Srad) and vapour pressure deficit (VPD) were calculated based on the temperature and precipitation for each forest grid point. A digital elevation map (100 m \times 100 m resolution) was required to address elevation and aspect-related variations in the interpolation procedure. For details on the algorithms, we refer to Petritsch and Hasenauer (2009).

A linear regression analysis of the interpolated grid point data revealed significant trends in the historic temperature for the period 1960–2009 (Table 1, results section). The average 50-year increase in temperature derived from the trends was 2.6 °C for T_{\min} and 1.4 °C for T_{\max} . The Prcp and VPD trends were not significant (Table 1, results section). Figure 2 shows for the period of 1960–2009 the regional distribution of the mean of daily average temperature [$(T_{\min} + T_{\max}) \times 0.5$], and the annual precipitation as well as the trends in average temperature and precipitation.

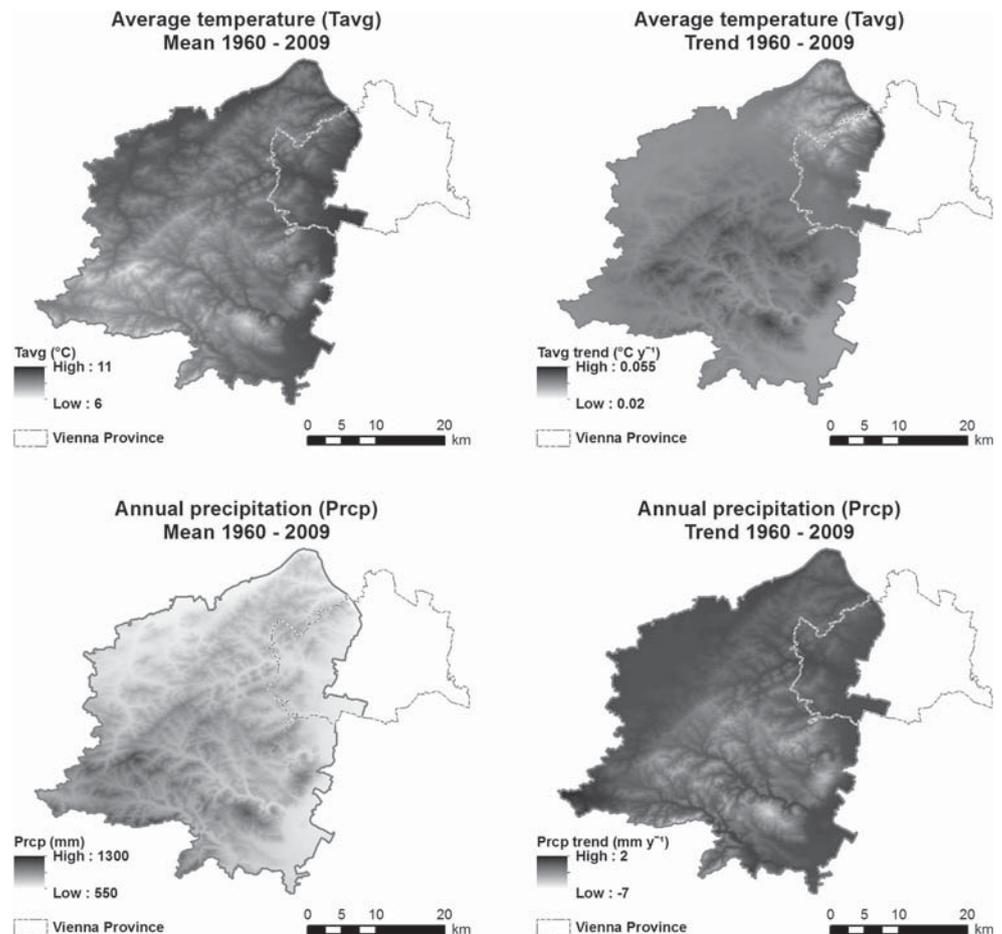
Climate change scenarios

The regional climate change scenarios were obtained from the regional climate model (RCM) climate limited-area model (CLM) v2.4.11 (Hollweg et al. 2008). CLM projections for Germany lie within the range of other regional climate change projections (Jacob et al. 2012; Deutscher Wetterdienst 2014). The experiments CLM_A1B_1_D3 and CLM_B1_1_D3 (Lautenschlager et al. 2009a, b) are European climate simulations on a 0.2° horizontal grid resolution (grid cell size \sim 15 km \times 22 km) for the years 2001–2100. They used global greenhouse gas emission scenarios A1B and B1 (IPCC 2000). The atmospheric CO₂ concentration in the A1B scenario is projected to reach 718 ppm, and 548 ppm in the B1 scenario by the end of the twenty-first century. The IPCC A1B scenario assumes a rapid economic growth, the global population peaking mid-century and an introduction of new and more efficient technologies affecting all energy sources. The B1 scenario addresses a high level of environmental and social consciousness, a fast change in economic structure towards a service and information economy combined with a coherent approach to sustainable development (low material, clean and resource-efficient technologies), but without additional climate initiatives. The global population also peaks mid-century and declines thereafter.

Daily T_{\min} , T_{\max} , Prcp and Srad data for the scenario A1B and B1 were obtained. They were not directly suitable as input for our ecosystem modelling because the RCM does not provide temperature and precipitation for single locations (the 782 forest grid points). Moreover, when switching from the observed daily weather data to the RCM scenario data, typically problematic discontinuities in the climate data occur. This phenomenon is especially pronounced in mountainous regions where discrepancies may be several degrees Celsius and more than 100 % in precipitation (Formayer et al. 2010).

For each day of the year, we calculated trend lines for T_{\min} , T_{\max} and Prcp by scenario to derive absolute changes between the years 2010 and 2100. The difference among the scenario grid cells turned out to be small; thus, we continued to use averaged values. Figure 3 gives the absolute T_{\min} and T_{\max} change for the scenario A1B and B1 for each day of the year. A polynomial regression was fit across all 365 daily changes. We obtained our 2010–2100 temperature scenarios time series for the 782 grid points by randomly repeating the meteorological years of the observation period 1960–2009 and then linearly increasing these T_{\min} and T_{\max} data with the smoothed daily temperature trends of the scenarios (Fig. 3). For Prcp and Srad, similar approaches were attempted. However, the changes yielded were negligible (not shown). Instead, we assumed Prcp to increase in winter and decrease in summer, its maximum at

Fig. 2 Mean average temperature (*top left*), annual average temperature change (*top right*), mean annual precipitation (*bottom left*) and annual precipitation change (*bottom right*) between 1960 and 2009. The data were calculated using DAYMET 100 m × 100 m grid interpolation. Average temperature calculated as the mean of daily minimum and maximum temperature. Trend calculated as the slope of the linear regression line through annual average values (temperature) or annual sums (precipitation)



30 % (Fig. 2). For Srad, we did not introduce a scenario because the projected changes were minor (not shown), but used the unchanged Srad values. VPD was calculated from the temperature scenarios using the DAYMET algorithm. All daily meteorological variables were always based on a common day from the observation period to ensure physical congruency. This resulted in four different climate change scenarios for the period 2010–2100:

1. A1B and no change in precipitation (A1B).
2. A1B and precipitation changes as outlined above (A1B + Prctp).
3. B1 and no change in precipitation (B1).
4. B1 and precipitation changes as outlined above (B1 + Prctp).

The linear trends of annual T_{\min} and T_{\max} , averaged for the 782 forest grid points for the period 2010–2100, gave a 100-year increase in T_{\min} of 4.2 °C and T_{\max} of 4.5 °C for A1B, and 2.3 °C (T_{\min}) and 2.6 °C (T_{\max}) for B1 (Table 1, results section). In Table 2 (results section), we provide the periodical mean values for the 20-year period 1960–1979, 1990–2009 and 2081–2100. Linear trends of Prctp for 2010–2100 were not significant, and VPD

increased significantly in both A1B and B1 (Table 1, results section). The residuals of the linear regression model for T_{\min} , T_{\max} , Prctp and VPD were analysed for temporal autocorrelation (using a Durbin-Watson test). No indication of our data not meeting the assumption of the regression analysis was found ($DW > 1.9$).

The annual average temperature development from 1960 to 2009 and from 2010 to 2100 for the A1B and B1 scenarios and the annual precipitation from 1960 to 2009 and from 2010 to 2100 with and without our precipitation scenario were averaged for all 782 forest grid points to show annual fluctuations and temporal developments (Fig. 4).

The ecosystem model

For our study, we used the ecosystem model Biome-BGC (Thornton 1998) version 4.1.1 (Thornton et al. 2002), with improvements related to species representation and the self-initialisation process (Pietsch et al. 2005; Pietsch and Hasenauer 2006). The model simulates energy, water, carbon and nitrogen cycles within a given ecosystem on a daily time step. The model is driven by the daily

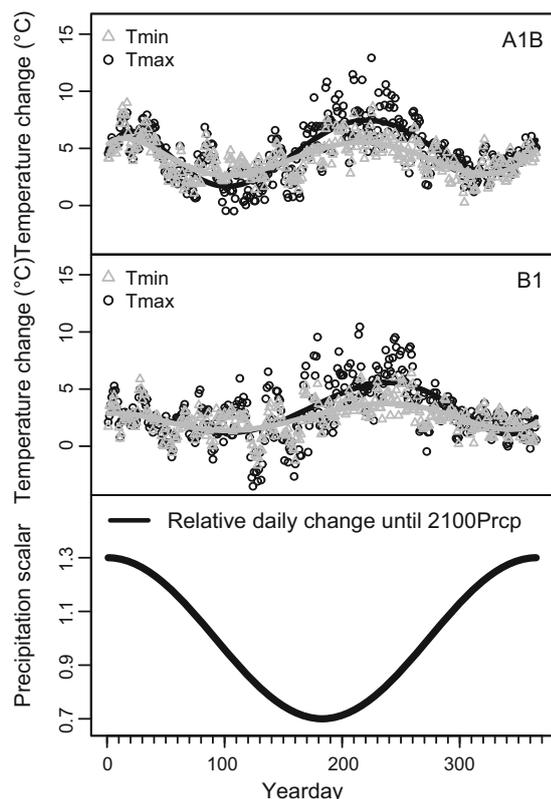


Fig. 3 Projected T_{\min} and T_{\max} change between 2010 and 2100 for each day of the year (lines polynomial regression) according to the CLM A1B (top) and B1 simulations (middle) and the sinusoidal scenario of relative precipitation change between 2010 and 2100 for each day of the year (bottom). The actual pattern of rainfall and non-rainfall days is retained

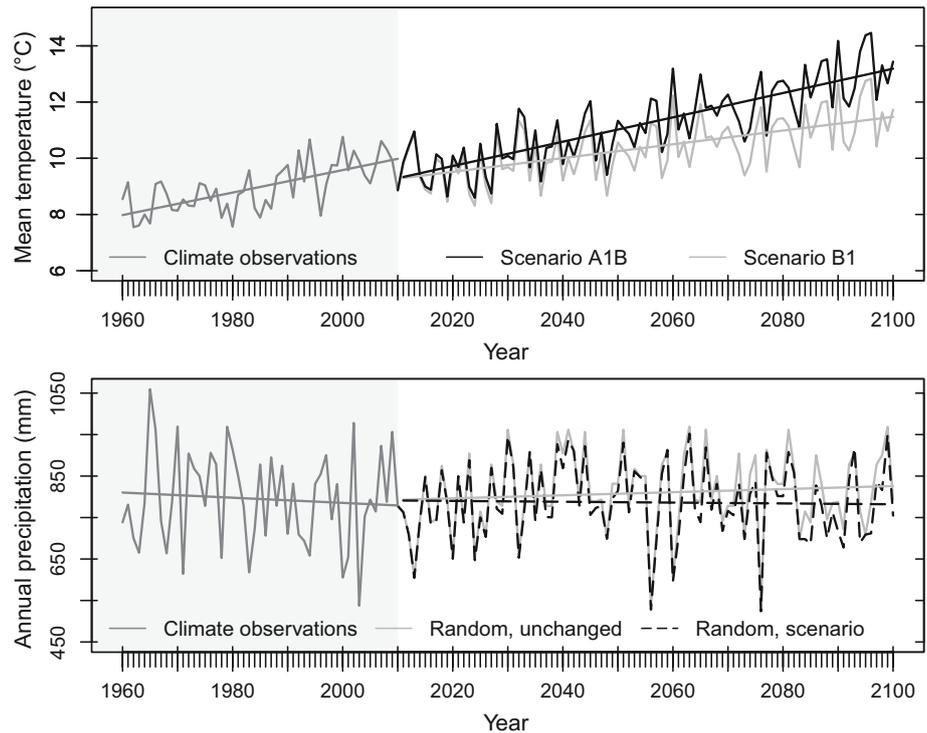
meteorological data, i.e. daily minimum and maximum temperature, incident solar radiation, vapour pressure deficit and precipitation. Vegetation-specific properties of the modelled ecosystem are listed in an ecophysiological parameter set (White et al. 2000; Pietsch et al. 2005). Atmospheric CO_2 content, nitrogen deposition and fixation, aspect, elevation and physical soil properties (depth, texture) are input parameters for the model. The model predicts stomatal conductance to CO_2 and water vapour by reducing species-specific maximum stomatal conductance by a series of multiplicative reductions based on solar radiation, VPD, soil water potential (Ψ , Ψ) and daily minimum temperature (Thornton et al. 2002). The multipliers take values from 1 (no limitation) to 0 (total stomatal closure). Threshold values of VPD [600, 3,000 Pa], Ψ [−0.34, −1.70 MPa] and T_{\min} [0, −8 °C] are species specific (Pietsch et al. 2005, values for beech in brackets). Photosynthesis is calculated separately for the sunlit and shaded canopy fractions, based on the Farquhar photosynthesis routine (Farquhar et al. 1980). Growth, the allocation of newly assimilated carbon to the different plant compartments and to the storage pools for following years

growth, is limited by the carbon requirements for auto-trophic respiration (i.e. for maintenance respiration, what needs to be fulfilled first, and for growth respiration) and by the availability of nitrogen to fulfil the species-specific C/N ratio requirements of the different plant compartments. Maintenance respiration is a temperature-dependent function of the nitrogen content of the plant compartment (Ryan 1991), and growth respiration is a function of the carbon allocated to the different plant compartments (Larcher 1995). Both leaves flushing in spring and litter-fall in autumn are soil temperature dependent. Decomposition of dead organic material is regulated by temperature and soil water status. Easily decomposable labile and more recalcitrant cellulose and lignin plant proportions go in different decomposition pathways. Leaching and volatile loss of and competition for soil mineral nitrogen between growing plants and decomposing microorganisms are considered in the model. The water cycle considers canopy interception and stomatal conductance/transpiration, evaporation from the canopy and from the soil, snow sublimation, storage of water in the soil and outflow (Of) of water exceeding saturation and field capacity. The soil water-holding capacity at saturation is derived from soil depth and texture, based on empirical pedotransfer functions (Clapp and Hornberger 1978; Cosby et al. 1984; Saxton et al. 1986). Evaporation and transpiration are estimated using the Penman–Monteith equation and depend on air temperature, air pressure, VPD, solar radiation and the transport resistance of water vapour and sensible heat; soil evaporation also depends on the number of days since the last rain event and transpiration on the stomatal, cuticular and boundary layer conductance. For further detail, we refer to Thornton (1998), White et al. (2000), Thornton et al. (2002), Pietsch and Hasenauer (2006) and Pietsch and Hasenauer (2009). For this study, phenology required an adaptation in order for it to account for altered phenology through increasing temperatures. Based on the original algorithm, we calculated the required long-term daily average temperature mean ($T_{\text{avg, mean}}$) from the available climate data (1960–2100) in a moving window that has the same length as the historic climate records (50 years).

Modelling procedure

The general modelling procedure within Biome-BGC uses a self-initialisation procedure including the dynamic mortality routine of Pietsch and Hasenauer (2006) to stabilise the pool sizes at a dynamic equilibrium (negligible changes i.e. in soil carbon stocks between two mortality cycles). Historic land use, i.e. forest management, was considered by a sequence of clear cuts and plantings (3–4) and thinnings for management-related impacts on the state and productivity of the forest system (Pietsch and Hasenauer

Fig. 4 Annual average temperature (*top*) and annual precipitation (*bottom*) averaged over the 782 forest grid points between 1960 and 2100, including linear trend lines. Values of the climate observation period 1960–2009 are interpolated with DAYMET. For temperature in the period 2010–2100, the meteorological years of the period 1960–2009 are randomly repeated and temperature is linearly increased with the A1B or B1 scenario temperature trends. For precipitation in the period 2010–2100, the meteorological years of the period 1960–2009 are randomly repeated or in addition rescaled with the sinusoidal precipitation scenario



2002). In this study, the rotation length was set to 130 years. Viennese forests experienced intensive management which was addressed by employing the thinning routine for beech as described in Petritsch (2008). For the scheduling of the management interventions, we randomly assigned a current age (in 2009) between 1 and 130 years to the simulation plots. The implemented forest management routine allows that during clear-cut and thinning intervention user-specified total amounts or shares of carbon and nitrogen are transferred from the living biomass pools (stem including branches, fine and coarse roots, leaves) to the dead biomass pools (coarse woody debris, litter), but carbon and nitrogen can also be extracted from the system.

The available daily climate data from 1960 to 2009 are repeatedly and randomly used for the simulations before 1960 (self-initialisation, historic land use). From 1960 to 2009, the observed climate data were used in the natural order, which is followed by the different climate change scenarios (A1B, A1B + Prcp, B1, B1 + Prcp). For the early phases of simulations, the CO₂ concentration was kept at a preindustrial level of 278 ppm. The historic anthropogenic CO₂ increase followed IPCC's mean global annual atmospheric CO₂ concentration data set IS92a starting in 1765 (IPCC 1992; Enting et al. 1994). For the climate change simulations, the CO₂ concentrations were used as prescribed by the emission scenarios A1B and B1. Preindustrial nitrogen deposition was estimated by Holland

et al. (1999) at 1 kg N ha⁻¹ year⁻¹, whereas current annual nitrogen deposition was taken from a nitrogen deposition map combining nitrogen deposited in wet and dry form, published by Eastaugh et al. (2011). The historic development of the nitrogen deposition was approximated by the trend in the atmospheric CO₂ concentration. For future simulations, the nitrogen deposition rates were kept constant at current levels. Soil texture and depth were interpolated from the Austrian National Forest Soil Survey (Petritsch and Hasenauer 2007).

Model validation

We obtained stand (age, volume) and site (elevation, slope, aspect) and management information for 32 experimental beech plots from the region which were established and are maintained by the Institute of Silviculture at the University of Natural Resources and Life Sciences, Vienna. Of these plots, ten are directly located within the study region. The remaining plots are found in the south within 65 km of the study area, and one plot is 120 km away. The experimental plots cover a wide age range (>150 years), have a documented management history and serve as model validation plots.

We applied the same modelling procedure as described above to the 32 experimental beech plots. The scheduling of the management, however, was adapted to the documented management history and the age of the plots.

Ecophysiological indicators

Daily weather, atmospheric CO₂ concentrations and nitrogen deposition rates affect the ecophysiological processes of forests either directly or through feedback between pools and fluxes. Certain ecophysiological indicators possess a strong ability to highlight potential reactions to changes in climate because they are decisive in the functioning and the productivity of forests. For our study, such model variables are the transpiration (Tr), the evaporation (Ev), the water use efficiency [WUE, ratio between net primary production (NPP) and transpiration], the soil water potential (Psi, Ψ), outflow of water through deep percolation (Of) and the net soil nitrogen mineralisation rate (Nmin). Psi is used by Biome-BGC as a surrogate for the leaf water potential. It can be taken as a measure of the system dryness. Furthermore, it influences the transpiration, evaporation, CO₂ uptake through the stomata and decomposition. Nmin is mediated by soil temperature and Psi and is important for sustained ecosystem productivity.

Ecosystem productivity indicators

Productivity indicators, such as leaf area index (LAI), gross primary production (GPP), NPP, the ratio NPP/GPP and net ecosystem exchange (NEE), are used to assess the potential productivity changes of forests. In our analysis, we covered the full heterogeneity in site productivity in the study region. Thus, we consider any reductions in productivity (carbon cycle) through the close link to other ecosystem processes and cycles (water, nitrogen, energy) as a potential threat to forest functioning and thus the provision of ecosystem services. This includes the provision of fresh air, shading and cooling, intact soil (mediated by the litter input and root growth) for proper filtering of drinking water, protection against soil erosion and flooding and the pleasure wandering about in a lush, healthy forest.

GPP strongly depend on daily weather, the nitrogen availability and feedback loops with LAI. The ratio NPP/GPP is a measure of the effective forest productivity. A decrease of NPP/GPP indicates a higher plant internal respiration and a lower biomass build-up. The total ecosystem carbon balance is given by the NEE (g C m⁻² day⁻¹). NEE is NPP reduced by heterotrophic respiration, which is dependent on temperature, soil water content and soil mineral nitrogen availability.

Analyses and results

Model validation

We applied Biome-BGC to the 32 experimental beech plots in the region. We converted the simulation results for stem

carbon to timber volume using biomass expansion factors (Pietsch et al. 2005) and compared the predicted volume with the observed stand volume (Fig. 5). The mean predicted and observed volumes are 362 and 364 m³ ha⁻¹, respectively. Standard deviation of the differences between predicted and observed values is 81 m³ ha⁻¹ or 22.2 % of the observed mean volume. The paired Student's *t* test revealed no significant difference between predicted and observed volume ($\Delta = -2$ m³ ha⁻¹, $t = 0.153 < t_{\alpha = 0.025, N = 31} = 2.04$). The linear regression analysis of observed versus predicted volume (Fig. 5) gives an r^2 of 0.80, an intercept of -34 m³ ha⁻¹ and a slope of 1.10. The volume residual analysis showed no trends versus elevation, slope, aspect and mean stand age (Fig. 5). The confidence (CI) and prediction intervals (PI) according to Reynolds (1984) revealed unbiased results, with a CI of -31 to $+27$ (-8.6 to $+7.4$ %) and a PI of -169 to $+165$ (-46.5 to $+45.3$ %). The CI examines divergences between the expected differences if the model is repeatedly used; the PI provides the range of the error in future applications. This suggests that Biome-BGC produces consistent and unbiased results and is a suitable diagnostic tool for our analysis.

Ecophysiological indicators

We calculated the ecophysiological indicators for the 782 forest grid points between 1960 and 2100. Linear regression (Table 1) and periodical mean values (Table 2) were calculated for the annual sums (Tr, Ev, Of, Nmin), annual means (WUE) or seasonal means (Ψ , mean for months June–August), averaged over all grid points. Annual evaporation is projected to increase in the A1B scenario, whereas transpiration is projected to decrease under A1B + Prcp and B1 + Prcp (Tables 1, 2) and so is the sum of Ev and Tr, evapotranspiration (ET, not shown). Annual WUE increased in every period and scenario (Tables 1, 2) and shows considerable annual variation (Fig. 6). In contrast, the summer time soil water potential shows persistent decrease, except for the B1 scenario (Tables 1, 2). The changes in mean monthly Psi between the 1960s and the 2090s are shown in Fig. 6, where the decrease in the summer months is apparent. Regional differences in mean summer Psi (Fig. 8c) and elevation trends (Fig. 9d–f) are evident. The annual Of from the bulk soil is projected to increase under A1B + Prcp and B1 + Prcp (Tables 1, 2). Net soil nitrogen mineralisation rates show a positive response to all four scenarios with highest rates in A1B, followed by A1B + Prcp (Tables 1, 2).

Ecosystem productivity indicators

The productivity indicators LAI, GPP, NPP and NEE for the period 1960–2100 were calculated for each of the 782 forest grid points (Fig. 7; Tables 1, 2). All four measures

Table 1 Slope parameter of the linear regression and result of the significance test for the trend using an $\alpha = 0.05$ (* = significant) for climate variables and ecophysiological and productivity indicators. Linear regression was done over the historic climate observation period and the future scenario period. All values are averages over the 782 forest grid points

Variables	1960–2009	2010–2100 A1B	2010–2100 A1B + Prcp	2010–2100 B1	2010–2100 B1 + Prcp
Climate variables					
T_{\min} (°C year ⁻¹)	0.0533*	0.0419*	0.0419*	0.0234*	0.0234*
T_{\max} (°C year ⁻¹)	0.0272*	0.0448*	0.0448*	0.0257*	0.0257*
Prcp (mm year ⁻²)	-0.5412	0.5319	0.0499	0.5319	0.0499
VPD (Pa year ⁻¹)	-0.064	2.124*	2.124*	1.3431*	1.3431*
Ecophysiological indicator					
Tr (mm year ⁻²)	0.7281	0.1633	-0.5941*	0.0789	-0.6606*
Ev (mm year ⁻²)	-0.1348	0.2571*	-0.0275	0.1456	-0.097
WUE (g C mm ⁻¹ year ⁻¹)	0.0023*	0.0022*	0.0032*	9.00E-04*	0.0017*
Psi (MPa year ⁻¹)	-0.0064	-0.0044*	-0.0068*	-0.0021	-0.0046*
Of (mm year ⁻²)	-1.1647	0.1092	0.6729*	0.3071	0.8115*
Nmin (g N m ⁻² year ⁻²)	-0.0015	0.0069*	0.0061*	0.0042*	0.0032*
Productivity indicator					
LAI (m ² m ⁻² year ⁻¹)	0.0117*	0.0076*	0.0021*	0.0032*	-0.002
GPP (g C m ⁻² year ⁻²)	3.0369*	2.4102*	1.2063*	1.0863*	-0.0301
NPP (g C m ⁻² year ⁻²)	1.6077*	1.015*	0.3209	0.4225	-0.2426
NPP/GPP (year ⁻¹)	-0.0004*	-0.0005*	-0.0005*	-0.0003*	-0.0003*
NEE (g C m ⁻² year ⁻²)	1.2695*	0.5364*	0.0621	0.1563	-0.2949

Variables are annual changes of annual average daily minimum temperature (T_{\min}), annual average daily maximum temperature (T_{\max}), annual precipitation (Prcp), annual average vapour pressure deficit (VPD), annual transpiration (Tr), annual evaporation (Ev), annual average water use efficiency (WUE = NPP/Tr), average June–August soil water potential (Psi), annual water outflow (Of), annual nitrogen mineralisation (Nmin), annual maximum leaf area index (LAI), annual gross primary production (GPP), annual net primary production (NPP), annual average net ecosystem exchange (NEE)

Table 2 Climate variables and ecophysiological and productivity indicators averaged over 20-year period during the historic climate observation period and the future scenario period. All values are averages over the 782 forest grid points

Variables	1960–1979	1990–2009	2081–2100 A1B	2081–2100 A1B + Prcp	2081–2100 B1	2081–2100 B1 + Prcp
Climate variables						
T_{\min} (°C)	3.7	5.4	8.2	8.2	6.7	6.7
T_{\max} (°C)	13	13.8	17.3	17.3	15.7	15.7
Prcp (mm year ⁻¹)	831	789	836	793	836	793
VPD (Pa)	557	553	732	732	670	670
Ecophysiological indicator						
Tr (mm year ⁻¹)	342	354	391	330	382	323
Ev (mm year ⁻¹)	228	226	249	227	241	221
WUE (g C mm ⁻¹)	1.12	1.21	1.33	1.41	1.24	1.31
Psi (MPa)	-0.44	-0.71	-0.89	-1.09	-0.7	-0.91
Of (mm year ⁻¹)	262	208	196	236	213	249
Nmin (g N m ⁻² year ⁻¹)	3.43	3.37	3.72	3.65	3.53	3.44
Productivity indicator						
LAI (m ² m ⁻²)	2.9	3.3	4	3.6	3.7	3.2
GPP (g C m ⁻² year ⁻¹)	605	691	896	800	793	704
NPP (g C m ⁻² year ⁻¹)	381	424	517	461	471	418
NPP/GPP (-)	0.63	0.61	0.58	0.58	0.59	0.59
NEE (g C m ⁻² year ⁻¹)	210	244	295	257	265	229

Variables are annual average daily minimum temperature (T_{\min}), annual average daily maximum temperature (T_{\max}), annual precipitation (Prcp), annual average vapour pressure deficit (VPD), annual transpiration (Tr), annual evaporation (Ev), annual average water use efficiency (WUE = NPP/Tr), average June–August soil water potential (Psi), annual water outflow (Of), annual nitrogen mineralisation (Nmin), annual maximum leaf area index (LAI), annual gross primary production (GPP), annual net primary production (NPP), annual average net ecosystem exchange (NEE)

Fig. 5 Volume observations versus predictions for validation plots including the trend analysis of standardised volume residuals versus site and stand parameters

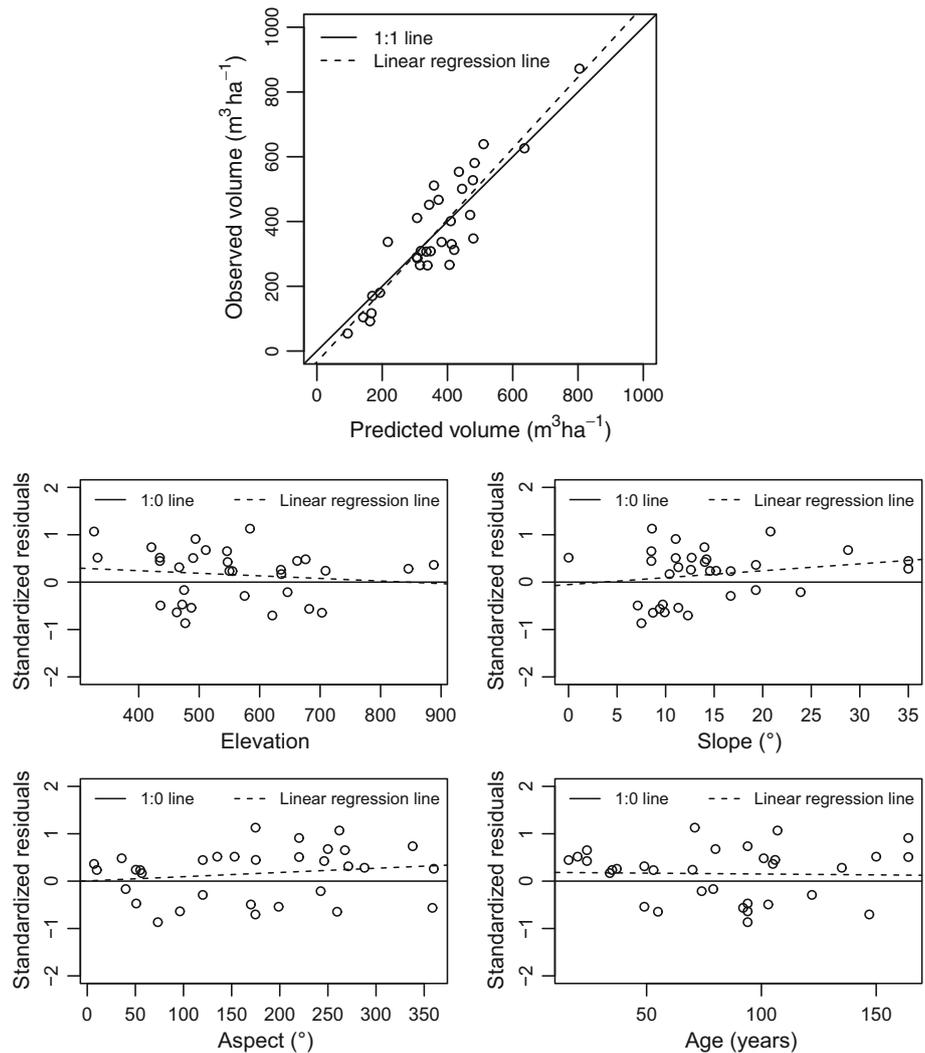


exhibit an increase for the period of 1960–2009. Among the climate change scenarios, A1B exhibits the highest increase for all indicators, whereas B1 + Prcp shows no change. A regional forest map with NPP averaged for 1990–2009 reveals the spatial variation of productivity in the region (Fig. 8a). Elevation gradients and differences between mean values for 1990–2009 and 2081–2100 are apparent (Fig. 9g–i). High productivity is apparent in the vicinity of Vienna, sub-region NE (Figs. 8a, 9g). A second map shows the relative changes of the period 2081–2100 versus 1990–2009 for A1B, the scenario with the highest productivity increase (Fig. 8b). The highest relative increase of up to 25 % is primarily found in high elevations (Figs. 8a, 9g–i). Under A1B + Prcp, NPP increases are less than half compared to the A1B scenario (Table 1; Fig. 9g–i). We calculated the correlation between the relative NPP increase (Fig. 8b) and the summer Psi (Fig. 8c). The correlation coefficient of 0.52 indicates strong correlation.

Discussion

Climatic effects

For the last 50 years (1960–2009), an increase in daily minimum temperature of 2.6 °C and in daily maximum temperature of 1.4 °C (Table 1) with large regional differences in the study area has been evident (Fig. 2). Until the end of the twenty-first century, climate change scenarios project an increase in average temperature of ~4.4 °C (A1B) and ~2.6 °C (B1); however, the projected changes vary for T_{\min} and T_{\max} , along with the seasons (Figs. 3, 4). Past (1960–2009) precipitation changes were not significant (Table 1), and CLM did not project strong Prcp trends for A1B and B1. Therefore, we conducted our study with unchanged Prcp and with our own Prcp scenario, assuming increased winter and decreased summer precipitation following assessments of the IPCC for Central Europe (Christensen et al. 2007).

Fig. 6 Modelled mean annual water use efficiency (WUE, NPP/transpiration, $\text{g C mm}^{-1} \text{H}_2\text{O}$) (top) and modelled monthly soil water potential (Psi, MPa) averaged for single decades (each tick indicates a month with Psi values averaged over the respective decade, bottom) using the historic climate observations and the two future temperature scenarios (A1B, B1) as well as a combined temperature—sinusoidal precipitation scenarios. Averaged over the 782 forest grid points

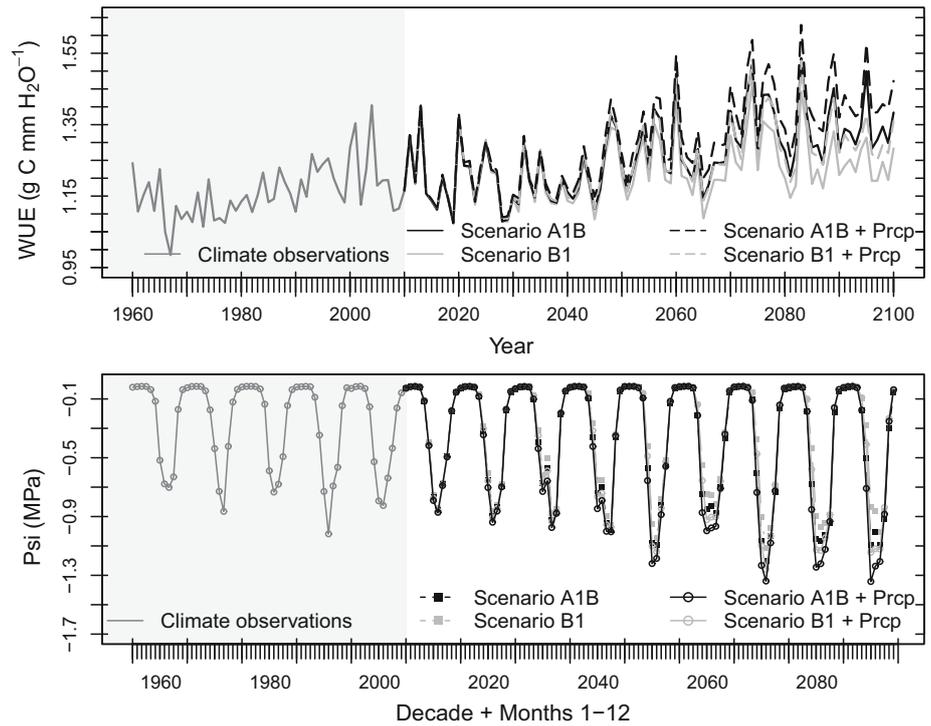
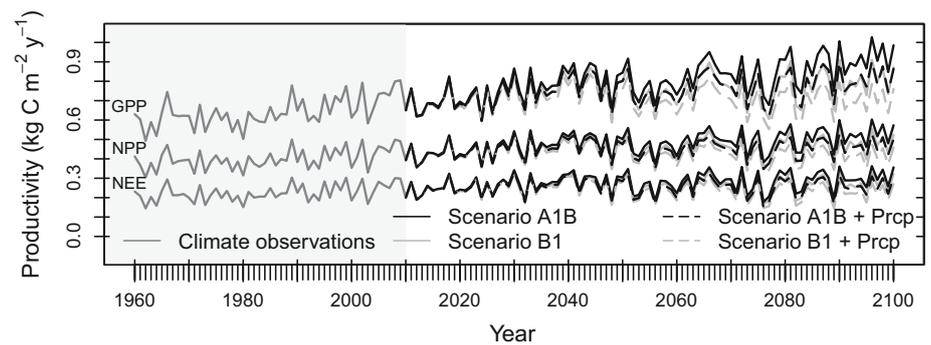


Fig. 7 Modelled average annual GPP, NPP and NEE using the historic climate observations and the two future temperature scenarios (A1B, B1) as well as a combined temperature—sinusoidal precipitation scenarios. Averaged over the 782 forest grid points

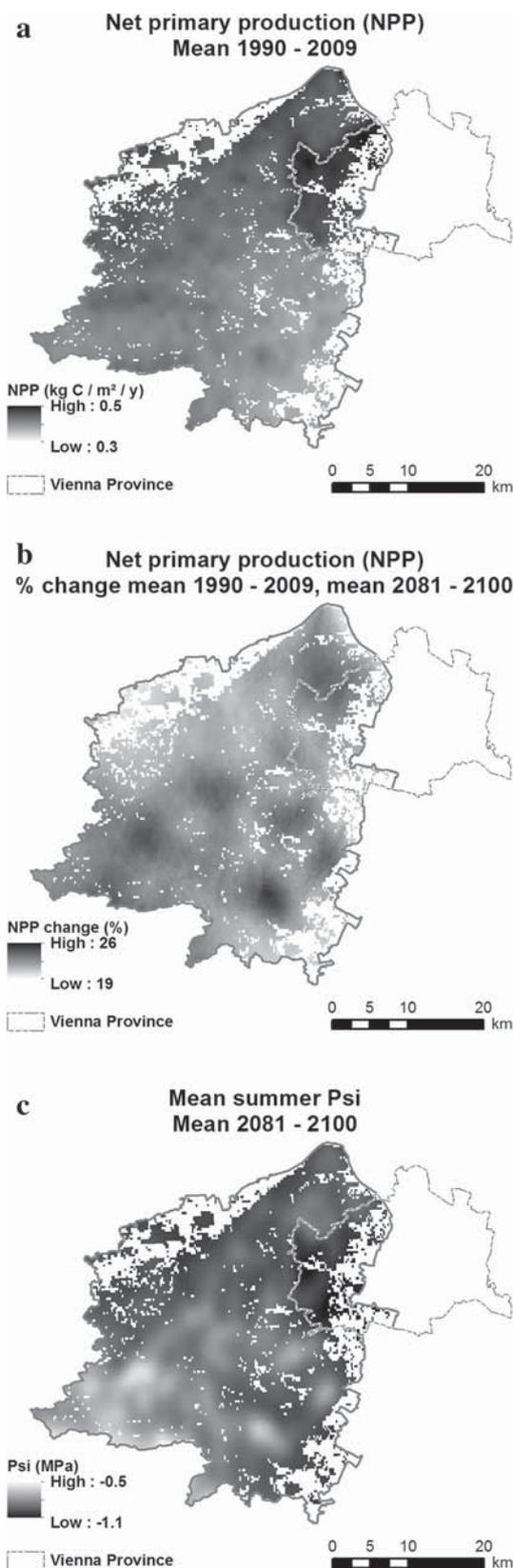


Higher temperatures have led to a prolongation of the growing season in Austria (Hasenauer et al. 1999) and can partly explain higher productivity in Austrian forests (Eastaugh et al. 2011). A moderate temperature increase fastens turnover and mineralisation processes (Lloyd and Taylor 1994) and therefore potentially increases ecosystem productivity. Overdieck et al. (2007), for example, show higher growth rates of juvenile beech trees with higher temperatures compared to growth rates at elevated CO_2 in a non-water-limited system. Temperature responses are represented by Biome-BGC in many of the modelled steps in the carbon and nitrogen cycles and include known negative effect of temperature on the carbon balance (Thornton 1998). For example, autotrophic respiration increases with temperature. Oxygenation reactions during photosynthesis (photorespiration) increase faster with temperature than

carboxylation reactions (CO_2 assimilation, Lambers et al. 2008). Higher maintenance respiration changes the carbon balance of forests and plays a significant role during the process of carbon starvation, where prolonged stomatal closure inhibits photosynthesis and carbon stores are depleted (McDowell et al. 2011). As an immediate effect of higher temperature, higher VPD (Tables 1, 2) increases the evaporative demand, the driving force for ET.

Impacts on ecophysiological indicators

Changes in the ET rates and precipitation patterns modify the Of (Tables 1, 2). In combination with a projected decrease in ET, an increase in stand Of is projected for A1B + Prcp and B1 + Prcp. The analysis of the sub-regions indicates that in both high and low elevations, our



◀**Fig. 8** (a) Mean annual NPP for the period 1990–2009 for the forested area in the study region and (b) relative annual NPP changes to the period 2081–2100, (c) and mean summer time (June–August) soil water potential Psi for the period 2081–2100 with the scenario A1B; interpolated with ArcGIS Kriging interpolation tools using the standard settings of ordinary Kriging

assumed Precp decrease in summer and increase in winter causes a decrease in ET and Of in summer but an increase in Of in winter (not shown), causing the increase in annual Of.

The WUE is projected to increase for all the scenarios, especially for A1B + Precp (Tables 1, 2). This confirms results of Forstreuter (2002), who experimentally found higher WUE for beech under elevated CO₂ concentrations and of Peñuelas et al. (2008), who detected increased intrinsic WUE with increasing CO₂ and temperature for mature beech trees in Catalonia (Davi et al. 2006) also predict continued increase of WUE for two French beech forest sites from 1960 to 2100.

We project lowered summer Psi for all but one scenario. The exception is the B1 scenario because neither Tr nor Ev are projected to change (Tables 1, 2). Regional differences in mean summer Psi under higher temperatures (Fig. 8c) are accompanied by strong elevation trends (Fig. 9d–f). This means drier soil conditions in low elevations and thus a stronger climate change impact, especially for the SE (SE sub-region). An additional decrease in summer Precp has a strong negative effect on the soil water status (Fig. 9d–f) and, in the following, stomatal conductance and thus CO₂ uptake are limited (compare following chapter). Low Psi also limits mineralisation processes. A correlation between annual Nmin and Psi, however, cannot be directly derived from our results because different trends in primary production and thus litter production disguise this effect.

Impacts on ecosystem productivity indicators

Depending on the scenario, the ecosystem productivity indicators LAI, GPP, NPP and NEE reveal a continued increase or preservation of the current productivity level (Fig. 7; Table 1). For both A1B and B1, the additional scenario of reduced summer and increased winter precipitation reduces LAI, GPP, NPP and NEE compared to the no-Precp change scenarios. This indicates a response to limited water supply during the growing season corresponding to the lower summer Psi (compare previous chapter). Spatial patterns in the productivity indicators are the result of the combined effect of spatially varying temperature, precipitation, soil properties and nutrient supply. The highest NPP values for the period 1990–2009 are evident for areas with high nitrogen deposition rates, such as the forests in the immediate vicinity of the city of Vienna (Figs. 8a, 9a, g). The analysis of the three sub-

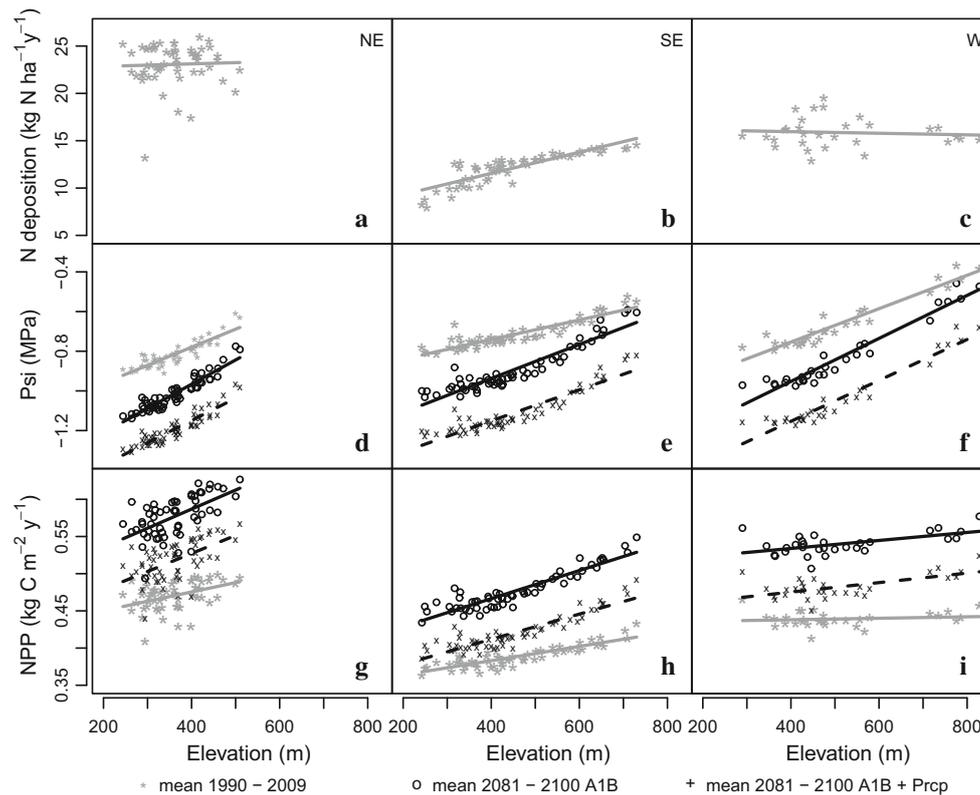


Fig. 9 Elevation trends for annual nitrogen deposition (a–c), summer (June–August) Psi (d–f) and annual NPP (g–i) averaged for the periods 1990–2009 and 2081–2100 for A1B and A1B + Prcp for

selected forest grid points from the sub-regions in the north-east (NE, a, d, g), south-east (SE, b, e, h) and west (W, c, f, i); sub-regions are defined in Fig. 1

regions (Fig. 1) reveals that responding to decreasing summer Psi towards lower elevations (Fig. 9d–f), annual NPP decreases with elevation (Fig. 9g–i). Therefore, the relative NPP increase (mean 2081–2100 compared to mean 1990–2009, shown for A1B or A1B + Prcp) is smaller in low elevations (Figs. 8b, c, 9g–i). The positive effect of increasing temperatures on productivity thus is more pronounced in higher elevations, whereas in lower elevations the productivity increase is limited by the water supply. The results are consistent with findings from the climate change impact study by Hlásný et al. (2011). They predict, using a multi-model approach, that beech forest productivity will increase in higher elevations but show less increase or even drought-induced decline in growth in the lower part of the species distribution range. The decreasing ratio NPP/GPP (Tables 1, 2) demonstrates a reduction in the efficiency of plant primary production because more carbon is required for maintenance respiration with increasing temperature. NEE (NPP minus heterotrophic respiration) is positive and increased during the past 50 years (Table 1). Although NEE is projected to further increase only together with increasing NPP (A1B), results suggest that the forest will remain a carbon sinks in all scenarios (Fig. 7). The underlying modelling assumptions are that timber is extracted during thinnings and final

harvest, whereas leaves and roots are left in the forest to decompose. The detected patterns in GPP and ecosystem respiration increase are consistent with reports from water and carbon fluxes of two French EUROFLUX beech sites (Davi et al. 2006) where in a climate sensitivity study up to 60 % GPP and 100 % NEE increase for the period 1960–2100 are projected.

A debated phenomenon in climate change impact studies is the downregulation of productivity due to nitrogen or generally nutrient limitation under CO₂ enrichment (Oren et al. 2001; Luo et al. 2004; Iversen and Norby 2008). Nutrient cycling, as implemented in Biome-BGC as a detailed nitrogen cycle, is important to detect possible downregulation of productivity (Medlyn et al. 2011). Our results show no clear sign of downregulation due to nitrogen limitation as the relative increase in NPP (Fig. 8b) is similar in regions with high N deposition (sub-region NE, inside city boundaries of Vienna, Fig. 9a) and areas with lower N deposition (e.g. lower elevations of sub-region SE; Fig. 9b). Also, increasing N mineralisation (Table 1) indicates no worsening nutrient limitation (Luo et al. 2004). Our results of no N limitation agree well with the estimated exceeding of the critical loads of eutrophication-causing nitrogen deposition by up to 15 kg N ha⁻¹ year⁻¹ in the study region (Obersteiner and Offenthaler 2008).

An uncertainty in the forest response to climate change is the potential limiting effect of elevated CO₂ on the stomatal conductance. Such a response is not included in Biome-BGC due to inconsistent results from field studies on woody species (Saxe et al. 1998; Norby et al. 1999; Thornton et al. 2002). Effects vary among plant functional groups and are generally lower for woody plant species than for grasses and herbaceous plants (Ainsworth and Rogers 2007). Also for *F. sylvatica*, the reports range from no response to conduction reductions of more than 30 % (Dufrêne et al. 1993; Liozon et al. 2000; Forstreuter 2002; Keel et al. 2007). Reduced stomatal conductance with elevated CO₂ could improve the WUE and increase productivity under water-limiting conditions (Saxe et al. 1998; Medlyn et al. 2011), but opposite results have also been reported (Warren et al. 2011).

In this climate change impact study, we did not model the risks of an increase in storm damage and the spread of forest-damaging agents (pathogens, insects), on the one hand, because storms and biotic disturbances are not part of the Biome-BGC model. On the other hand, susceptibility to storm damage is low for beech, compared to other dominant tree species, for example, Norway spruce (Schütz et al. 2006; Thom et al. 2013). Beech is also considered less susceptible to biotic damaging agents, although several different beech pests and pathogens are known (Steyrer 2009; Tomiczek et al. 2011). They include a number of secondary damaging agents (that follow drought periods and wind damages), which research pays special attention to at the xeric edge of the natural distribution range of beech (Lakatos and Molnár 2009; Rasztovits et al. 2013). A recent study in the biosphere reserve Vienna Woods, however, found no bark beetle damage even on wind-throw sites (Steyrer and Wieshaider 2010).

Forest management planning may be influenced by drought effects and require heightened attention to stand structure, harvesting regimes and (ground-) water management in the future (Lindner et al. 2010; Seidl et al. 2011; Hlásny et al. 2014). For this study, we did not consider alternatives to our implemented forest management routine. A careful adaptation of the shelterwood system may be necessary under climate change for Chakraborty et al. (2013) report a higher risk of crown dieback and even total mortality in dry years for beech regeneration in the understory of adult trees due to competition for water. Since Biome-BGC does not simulate different tree layers, this effect could not be tested. Alternative future management scenarios could also include increased biomass extraction for energy production (e.g. fine branches or leaves), consequently changing NEE and the nutrient cycle, or shortened rotation periods to make use of the increasing productivity. Shortened rotation periods could reduce the risk of red heartwood in the beech stems that develops with

age (Knoke 2003) and also reduce the risk of disturbances (i.e. storms).

Impacts on welfare and recreation

The projected impact of climate change on ecophysiology and productivity and thus on forest functions of the Vienna Woods may have implications on welfare and recreation.

The projected reduction in transpiration (Tables 1, 2) will reduce evaporative cooling in the canopy. The extent to which this cooling in the canopy will effect potential cooling effects within a forest stand is difficult to assess (Oke et al. 1989). Changes in the ET rates, precipitation patterns and WUE are projected to influence Of and thus potentially drinking water sources (Tables 1, 2). Our projections of stable productivity (see Fig. 7; Table 1) fulfil the very general requirement of stable forests for sustainable drinking water supply (Richards et al. 2012). The preservation of beech forests is beneficial because of its high effectiveness in filtering out nitrates that typically harm drinking water quality (von Wilpert et al. 2000). Following Bartsch (2000), problems with drinking water quality cannot be excluded, where forests on shallow soils are disturbed and low pH in the surface soil increases nitrate leaching and hinders fast vegetation growth after gap creation.

The projected increase in LAI (Table 2) may have several positive implications: (1) a high LAI is important for flood protection because water is intercepted, evaporated and transpired, and thus, run-off rates are reduced (Badoux et al. 2006; Pötzelsberger and Hasenauer 2015); (2) a well-developed canopy provides shade for recreation seeking visitors; (3) a high LAI guarantees continued litter production, and therefore, an organic-rich well-structured soil that filters, adsorbs and transforms pollutants and therefore is important for clean drinking water supply (Dudley and Stolton 2003; Blume et al. 2010). Such a well-developed soil, in combination with a dense canopy and litter layer, is also more resistant to erosion (Brang et al. 2001; Salles et al. 2002).

NEE is projected to stay positive under all climate change scenarios and of unaltered forest management, implying that these forests act as carbon sinks and thus help mitigating climate change. In a strict sense, this climate change mitigation effect applies to a situation, where the extracted wood is stored permanently and is not burned or left to decompose somewhere outside the forest.

Conclusion

With biogeochemical mechanistic ecosystem modelling, we were able to project changes in ecophysiological and

productivity indicators for the Vienna Woods under two different temperature scenarios combined with two variants for precipitation (increased winter and decreased summer precipitation, or no change). Changes in the carbon, water and nutrient pools and fluxes are diverse due to multiple feedback loops and different temperature dependencies of biological and geochemical processes. Changes in precipitation pattern plus temperature increase are projected to decrease annual ET, increase the WUE and increase water Of in winter. Annual NPP and NEE are projected to increase for one of the four scenarios. Lower summer soil water potentials especially in lower elevations limit the productivity increase. Overall, we project that the Vienna Woods will continue to fulfil their key forest functions.

Acknowledgments This work was financed by the City of Vienna in support of the EFI Central-East European Regional Office. Our thanks goes to Ervin Rasztovits and Norbert Móricz for their support in retrieving the CLM climate change scenario data. We thank Roland Köck and two anonymous reviewers for their valuable comments and Adam Moreno for English editing.

References

- Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant Cell Environ* 30:258–270. doi:10.1111/j.1365-3040.2007.01641.x
- Albrecht FK (2011) GIS-gestützte Analyse der gesellschaftlichen Leistungen des Wiener Wald- und Wiesengürtels (GIS aided analysis of the social services of the Greenbelt Vienna). Master thesis, University of Natural Resources and Life Sciences, Vienna
- Badoux A, Witzig J, Germann PF et al (2006) Investigations on the runoff generation at the profile and plot scales, Swiss Emmental. *Hydrol Process* 20:377–394. doi:10.1002/hyp.6056
- Bartsch N (2000) Element release in beech forest gaps. *Water Air Soil Pollut* 122:3–16
- Blume H-P, Brümmner GW, Horn R et al (2010) Scheffer/Schachtschabel Lehrbuch der Bodenkunde (Textbook of soil science), 16th edn. Spektrum Akademischer Verlag, Heidelberg
- Brang P, Schönenberger W, Ott E, Gardner B (2001) Forests as protection from natural hazards. In: Evans J (ed) *Forest handbook*. Blackwell Science, Oxford, pp 53–81
- Carreiro MM, Song Y-C, Wu J (2008) Ecology, planning, and management of urban forests: an international perspective. Springer, New York
- Chakraborty T, Saha S, Reif A (2013) Decrease in available soil water storage capacity reduces vitality of young understorey European Beeches (*Fagus sylvatica* L.)—a case study from the Black Forest, Germany. *Plants* 2:676–698. doi:10.3390/plants2040676
- Christensen JH, Hewitson B, Busuioc A et al (2007) Regional climate projections. In: Solomon S, Qin D, Manning M et al (eds) *Climate change 2007: physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, pp 847–940
- Clapp RB, Hornberger GM (1978) Empirical equations for some soil hydraulic properties. *Water Resour Res* 14:601–604. doi:10.1029/WR014i004p00601
- Cosby BJ, Hornberger GM, Clapp RB, Ginn TR (1984) A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resour Res* 20:682–690. doi:10.1029/WR020i006p00682
- Davi H, Dufrière E, Francois C et al (2006) Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. *Agric For Meteorol* 141:35–56. doi:10.1016/j.agrformet.2006.09.003
- Deutscher Wetterdienst (2014) Regionaler Klimawandel—Klimamodelle im Vergleich (Regional climate change—comparison of climate models). http://www.dwd.de/bvbw/appmanager/bvbw/dwd/www/Desktop?_nfpb=true&_pageLabel=dwdwww_start&T99803827171196328354269gsbDocumentPath=Navigation/Oeffentlichkeit/Homepage/Klimawandel/ZWEK__T__node.html?__nnn=true. (Accessed 16 Dec 2014)
- Dobbs C, Escobedo FJ, Zipperer WC (2011) A framework for developing urban forest ecosystem services and goods indicators. *Landsc Urban Plan* 99:196–206. doi:10.1016/j.landurbplan.2010.11.004
- Dudley N, Stolton S (2003) Running pure: the importance of forest protected areas to drinking water. The World Bank/WWF International, Washington D.C., USA
- Dufrière E, Pontallier J-Y, Saugier B (1993) A branch bag technique for simultaneous CO₂ enrichment and assimilation measurements on beech (*Fagus sylvatica* L.). *Plant Cell Environ* 16:1131–1138. doi:10.1111/j.1365-3040.1996.tb02071.x
- Dukes JS, Pontius J, Orwig D et al (2009) Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Can J For Res* 39:231–248. doi:10.1139/X08-171
- Eastaugh CS, Pötzelsberger E, Hasenauer H (2011) Assessing the impacts of climate change and nitrogen deposition on Norway spruce (*Picea abies* L. Karst) growth in Austria with BIOME-BGC. *Tree Physiol* 31:262–274. doi:10.1093/treephys/tpr033
- Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen* (Vegetation ecology of central Europe), 6th edn. Ulmer, Stuttgart
- Enting IG, Wigley TML, Heimann M, Scientific C (1994) Future emissions and concentrations of carbon dioxide: key ocean/atmosphere/land analyses. Division of Atmospheric Research technical paper no. 31. CSIRO, Australia
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 species. *Planta* 149:78–90
- Foet M-C (2010) Der Wiener Grüngürtel: Leistungen und Nutzen für die Gesellschaft (The Vienna green belt). Master thesis, University of Natural Resources and Life Sciences, Vienna
- Formayer H, Haas P, Nadeem I (2010) Regional climate model scenarios of CC-WaterS. Explanatory report. University of Natural Resources and Life Sciences, Vienna
- Forstreuter M (2002) Auswirkungen globaler Klimaänderungen auf das Wachstum und den Gaswechsel (CO₂/H₂O) von Rotbuchenbeständen (*Fagus sylvatica* L.) (Impacts of global climate change on the growth and gas exchange of European beech stands). *Landschaftsentwicklung und Umweltforschung - Schriftenreihe der Fakultät VII Architektur Umwelt Gesellschaft*, 119, Technische Universität Berlin
- Furniss MJ, Staab BP, Hazelhurst S et al (2010) Water, climate change, and forests. US Department of Agriculture, Forest Service, Pacific Northwest Research Station
- Granier A, Reichstein M, Bréda N et al (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agric For Meteorol* 143:123–145. doi:10.1016/j.agrformet.2006.12.004
- Hasenauer H, Nemani RR, Schadauer K, Running SW (1999) Forest growth response to changing climate between 1961 and 1990 in

- Austria. *For Ecol Manag* 122:209–219. doi:10.1016/S0378-1127(99)00010-9
- Hasenauer H, Merganicova K, Petritsch R et al (2003) Validating daily climate interpolations over complex terrain in Austria. *Agric For Meteorol* 119:87–107. doi:10.1016/S0168-1923(03)00114-X
- Hlásny T, Barcza Z, Fabrika M et al (2011) Climate change impacts on growth and carbon balance of forests in Central Europe. *Clim Res* 47:219–236. doi:10.3354/cr01024
- Hlásny T, Barcza Z, Barka I et al (2014) Future carbon cycle in mountain spruce forests of Central Europe: modelling framework and ecological inferences. *For Ecol Manag* 328:55–68. doi:10.1016/j.foreco.2014.04.038
- Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46:7–43. doi:10.1007/BF01007572
- Hollweg H-D, Böhm U, Fast I et al (2008) Ensemble simulations over Europe with the regional climate model CLM forced with IPCC AR4 global scenarios. Technical report 3. Max-Planck-Institut für Meteorologie, Hamburg
- Hyvönen R, Ågren GI, Linder S et al (2006) The likely impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytol* 173:463–480
- IPCC (1992) Climate change 1992: the supplementary report to the IPCC scientific assessment. Cambridge University Press, Cambridge
- IPCC (2000) Emission scenarios: a special report of IPCC working group III. Cambridge University Press, Cambridge
- Iversen CM, Norby RJ (2008) Nitrogen limitation in a sweetgum plantation: implications for carbon allocation and storage. *Can J For Res* 38:1021–1032. doi:10.1139/X07-213
- Jacob D, Bülow K, Kotova L et al (2012) Climate Service Center report 6, Regionale Klimaprojektionen für Europa und Deutschland: Ensemble-Simulationen für die Klimafolgenforschung. Climate Service Center, Hamburg
- Keel SG, Pepin S, Leuzinger S, Körner C (2007) Stomatal conductance in mature deciduous forest trees exposed to elevated CO₂. *Trees* 21:151–159. doi:10.1007/s00468-006-0106-y
- Knoke T (2003) Predicting red heartwood formation in beech trees (*Fagus sylvatica* L.). *Ecol Model* 169:295–312. doi:10.1016/S0304-3800(03)00276-X
- Konijnendijk CC (2008) The forest and the city: the cultural landscape of urban woodland. Springer, New York
- Konijnendijk C, Nilsson K, Randrup T, Schipperijn J (2005) Urban forests and trees: a reference book. Springer, Berlin
- Koukal T (2004) Nonparametric assessment of forest attributes by combination of field data of the Austrian forest inventory and remote sensing data. PhD thesis, University of Natural Resources and Life Sciences, Vienna
- Lakatos F, Molnár M (2009) Mass Mortality of Beech (*Fagus sylvatica* L.) in South-West Hungary. *Acta Silv Lign Hung* 5:75–82
- Lambers H, Chapin FS, Pons TL (2008) Plant physiological ecology, 2nd edn. Springer, New York
- Landsteiner V (1990) Wienerwald (Vienna Woods). Österreichische Bundesforste (Austrian Federal Forests), Vienna
- Larcher W (1995) Physiological plant ecology. Springer, Berlin
- Larsson T-B (2001) Ecological bulletins 50: biodiversity evaluation tools for European forests. Wiley, Hoboken
- Lautenschlager M, Keuler K, Wunram C et al (2009a) Climate simulation with CLM, scenario A1B run no. 1, data stream 3: European region MPI-M/MaD. World Data Center for Climate, Hamburg. doi:10.1594/WDCC/CLM_A1B_1_D3
- Lautenschlager M, Keuler K, Wunram C et al (2009b) Climate simulation with CLM, scenario B1 run no. 1, data stream 3: European region MPI-M/MaD. World Data Center for Climate, Hamburg. doi:10.1594/WDCC/CLM_B1_1_D3
- Lindner M, Maroschek M, Netherer S et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For Ecol Manag* 259:698–709. doi:10.1016/j.foreco.2009.09.023
- Liozon R, Badeck F, Genty B et al (2000) Leaf photosynthetic characteristics of beech (*Fagus sylvatica*) saplings during three years of exposure to elevated CO₂ concentration. *Tree Physiol* 20:239–247
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Funct Ecol* 8:315–323
- Luo Y, Su B, Currie WS et al (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* 54:731–739. doi:10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2
- Luo Y, Gerten D, Le Maire G et al (2008) Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Glob Chang Biol* 14:1986–1999. doi:10.1111/j.1365-2486.2008.01629.x
- Mátyás C, Berki I, Czúcz B et al (2010) Future of beech in southeast Europe from the perspective of evolutionary ecology. *Acta Silv Lign Hung* 6:91–110
- McDowell NG, Beerling DJ, Breshears DD et al (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol Evol* 26:523–532. doi:10.1016/j.tree.2011.06.003
- Medlyn BE, Duursma RA, Zeppel MJB (2011) Forest productivity under climate change: a checklist for evaluating model studies. *Wiley Interdiscip Rev Clim Chang* 2:332–355. doi:10.1002/wcc.108
- Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecol Appl* 17:2145–2151
- Norby RJ, Wullschlegel SD, Gunderson CA et al (1999) Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell Environ* 22:683–714
- Obersteiner E, Offenthaler I (2008) Critical Loads für Schwefel- und Stickstoffeinträge in Ökosysteme (Critical loads for sulfur and nitrogen deposition in ecosystems). Environment Agency Austria (Umweltbundesamt), Vienna
- Oke TR, Crowther JM, McNaughton KG et al (1989) The micrometeorology of the urban forest [and discussion]. *Philos Trans R Soc B Biol Sci* 324:335–349. doi:10.1098/rstb.1989.0051
- Oleyar MD, Greve AI, Withey JC, Bjorn AM (2008) An integrated approach to evaluating urban forest functionality. *Urban Ecosyst* 11:289–308. doi:10.1007/s11252-008-0068-5
- Oren R, Ellsworth DS, Johnsen KH et al (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* 411:469–472. doi:10.1038/35078064
- Overdieck D, Ziche D, Böttcher-Jungclaus K (2007) Temperature responses of growth and wood anatomy in European beech saplings grown in different carbon dioxide concentrations. *Tree Physiol* 27:261–268
- Peñuelas J, Ogaya R, Boada M, Jump AS (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30:829–837. doi:10.1111/j.2007.0906-7590.05247.x
- Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008) Twentieth century changes of tree-ring δ¹³C at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Glob Chang Biol* 14:1076–1088. doi:10.1111/j.1365-2486.2008.01563.x
- Peters EB, McFadden JP (2010) Influence of seasonality and vegetation type on suburban microclimates. *Urban Ecosyst* 13:443–460. doi:10.1007/s11252-010-0128-5

- Petritsch R (2002) Anwendung und Validierung des Klimainterpolationsmodells DAYMET in Österreich (Application and validation of the climate interpolation model DAYMET in Austria). Master thesis, University of Natural Resources and Life Sciences, Vienna
- Petritsch R (2008) Large scale mechanistic ecosystem modeling in Austria. PhD thesis, University of Natural Resources and Life Sciences, Vienna
- Petritsch R, Hasenauer H (2007) Interpolating input parameters for large scale ecosystem models. *Austrian J For Sci* 124:135–151
- Petritsch R, Hasenauer H (2009) Tägliche Wetterdaten im 1 km Raster von 1960 bis 2008 über Österreich (Gridded Daily weather data between 1960 and 2008 across Austria). *Austrian J For Sci* 126:215–225
- Pietsch SA, Hasenauer H (2002) Using mechanistic modeling within forest ecosystem restoration. *For Ecol Manag* 159:111–131. doi:10.1016/S0378-1127(01)00714-9
- Pietsch SA, Hasenauer H (2006) Evaluating the self-initialization procedure for large-scale ecosystem models. *Glob Chang Biol* 12:1658–1669. doi:10.1111/j.1365-2486.2006.01211.x
- Pietsch SA, Hasenauer H (2009) Photosynthesis within large-scale ecosystem models. In: Laïsk A, Nedbal L, Govindjee (eds) *Advances in photosynthesis and respiration. Photosynthesis in silico*, vol 29. Springer, Dordrecht, pp 441–464
- Pietsch SA, Hasenauer H, Thornton PE (2005) BGC-model parameters for tree species growing in central European forests. *For Ecol Manag* 211:264–295. doi:10.1016/j.foreco.2005.02.046
- Pötzelsberger E, Hasenauer H (2015) Forest—water dynamics within a mountainous catchment in Austria. *Nat Hazards*. doi:10.1007/s11069-015-1609-x
- Pretzsch H, Biber P, Schütze G et al (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat Commun* 5:4967. doi:10.1038/ncomms5967
- Rasztovits E, Berki I, Mátyás C et al (2013) The incorporation of extreme drought events improves models for beech persistence at its distribution limit. *Ann For Sci* 71:201–210. doi:10.1007/s13595-013-0346-0
- Renner M, Sweeney S, Kubit J (2008) Green jobs: towards decent work in a sustainable, low-carbon world. UNEP, Nairobi
- Reynolds MR (1984) Estimating the error in model predictions. *For Sci* 30:454–469
- Richards WH, Koeck R, Gersonde R et al (2012) Landscape-scale forest management in the municipal watersheds of Vienna, Austria, and Seattle, USA: commonalities despite disparate ecology and history. *Nat Areas J* 32:199–207
- Ryan MG (1991) Effects of climate change on plant respiration. *Ecol Appl* 1:157–167
- Salles C, Poesen J, Sempere-Torres D (2002) Kinetic energy of rain and its functional relationship with intensity. *J Hydrol* 257:256–270. doi:10.1016/S0022-1694(01)00555-8
- Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytol* 139:395–436
- Saxton KE, Rawls WJ, Romberger JS, Papendick RI (1986) Estimating generalized soil-water characteristics from texture. *Soil Sci Soc Am J* 50:1031. doi:10.2136/sssaj1986.03615995005000040039x
- Schütz J-P, Götz M, Schmid W, Mandallaz D (2006) Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. *Eur J For Res* 125:291–302. doi:10.1007/s10342-006-0111-0
- Seidl R, Rammer W, Lexer MJ (2011) Climate change vulnerability of sustainable forest management in the Eastern Alps. *Clim Chang* 106:225–254. doi:10.1007/s10584-010-9899-1
- Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nat Clim Chang* 4:806–810. doi:10.1038/nclimate2318
- Steyrer G (2009) Buchenborkenkäfer: Projekt im Biosphärenpark Wienerwald (Beech bark beetle: project in the biosphere reserve Vienna Woods). *For Aktuell* 45:9–11
- Steyrer G, Wieshaider A (2010) Entwarnung im Biosphärenpark Wienerwald: derzeit keine Massenvermehrung des Buchenborkenkäfers (All-clear in the biosphere reserve Vienna Woods: currently no mass outbreak of the beech bark beetle). BFW-Austrian Research Centre For, Vienna. <http://bfw.ac.at/rz/bfwcms2.web?dok=8538>. (Accessed 16 Oct 2014)
- Tegel W, Seim A, Hakelberg D et al (2013) A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. *Eur J For Res* 133:61–71. doi:10.1007/s10342-013-0737-7
- Thom D, Seidl R, Steyrer G et al (2013) Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *For Ecol Manag* 307:293–302. doi:10.1016/j.foreco.2013.07.017
- Thornton PE (1998) Regional ecosystem simulation: combining surface- and satellite-based observations to study linkages between terrestrial energy and mass budgets. PhD thesis, University of Montana, Missoula
- Thornton PE, Running SW, White M (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251. doi:10.1016/S0022-1694(96)03128-9
- Thornton PE, Hasenauer H, White M (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric For Meteorol* 104:255–271. doi:10.1016/S0168-1923(00)00170-2
- Thornton PE, Law BE, Gholz HL et al (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric For Meteorol* 113:185–222. doi:10.1016/S0168-1923(02)00108-9
- Tomiczek C, Perny B, Cech TL (2011) Zur Waldschuttsituation der Buche (Forest pests and diseases of beech). BFW-Praxisinformation 12:19–21
- Von Wilpert K, Zirlewagen D, Kohler M (2000) To what extent can silviculture enhance sustainability of forest sites under the immission regime in Central Europe. *Water Air Soil Pollut* 122: 105–120
- Warren JM, Norby RJ, Wullschlegel SD (2011) Elevated CO₂ enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiol* 31:117–130. doi:10.1093/treephys/tpr002
- White M, Thornton PE, Running SW, Nemani RR (2000) Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4:1–85. doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2
- Woodall CW, Nowak DJ, Liknes GC, Westfall JA (2010) Assessing the potential for urban trees to facilitate forest tree migration in the eastern United States. *For Ecol Manag* 259:1447–1454. doi:10.1016/j.foreco.2010.01.018
- Young RF (2010) Managing municipal green space for ecosystem services. *Urban For Urban Green* 9:313–321. doi:10.1016/j.ufug.2010.06.007
- Zheng D, Ducey MJ, Heath LS (2013) Assessing net carbon sequestration on urban and community forests of northern New England, USA. *Urban For Urban Green* 12:61–68. doi:10.1016/j.ufug.2012.10.003