

Potsdam Institute for Climate Impact Research
RD II

**Model-based analysis of climate change impacts on the productivity of
oak-pine forests in Brandenburg**

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Abstract

The relationship between climate and forest productivity is an intensively studied subject in forest science. This Thesis is embedded within the general framework of future forest growth under climate change and its implications for the ongoing forest conversion. My objective is to investigate the future forest productivity at different spatial scales (from a single specific forest stand to aggregated information across Germany) with focus on oak-pine forests in the federal state of Brandenburg. The overarching question is: how are the oak-pine forests affected by climate change described by a variety of climate scenarios. I answer this question by using a model-based analysis of tree growth processes and responses to different climate scenarios with emphasis on drought events. In addition, a method is developed which considers climate change uncertainty of forest management planning.

As a first 'screening' of climate change impacts on forest productivity, I calculated the change in net primary production on the base of a large set of climate scenarios for different tree species and the total area of Germany. Temperature increases up to 3 K lead to positive effects on the net primary production of all selected tree species. But, in water-limited regions this positive net primary production trend is dependent on the length of drought periods which results in a larger uncertainty regarding future forest productivity. One of the regions with the highest uncertainty of net primary production development is the federal state of Brandenburg.

To enhance the understanding and ability of model based analysis of tree growth sensitivity to drought stress two water uptake approaches in pure pine and mixed oak-pine stands are contrasted. The first water uptake approach consists of an em-

pirical function for root water uptake. The second approach is more mechanistic and calculates the differences of soil water potential along a soil-plant-atmosphere continuum. I assumed the total root resistance to vary at low, medium and high total root resistance levels. For validation purposes three data sets on different tree growth relevant time scales are used. Results show that, except the mechanistic water uptake approach with high total root resistance, all transpiration outputs exceeded observed values. On the other hand high transpiration led to a better match of observed soil water content. The strongest correlation between simulated and observed annual tree ring width occurred with the mechanistic water uptake approach and high total root resistance. The findings highlight the importance of severe drought as a main reason for small diameter increment, best supported by the mechanistic water uptake approach with high root resistance. However, if all aspects of the data sets are considered no approach can be judged superior to the other. I conclude that the uncertainty of future productivity of water-limited forest ecosystems under changing environmental conditions is linked to simulated root water uptake.

Finally my study aimed at the impacts of climate change combined with management scenarios on an oak-pine forest to evaluate growth, biomass and the amount of harvested timber. The pine and the oak trees are 104 and 9 years old respectively. Three different management scenarios with different thinning intensities and different climate scenarios are used to simulate the performance of management strategies which explicitly account for the risks associated with achieving three predefined objectives (maximum carbon storage, maximum harvested timber, intermediate). I found out that in most cases there is no general management strategy which fits best to different objectives. The analysis of variance in the growth related model

outputs showed an increase of climate uncertainty with increasing climate warming. Interestingly, the increase of climate-induced uncertainty is much higher from 2 to 3 K than from 0 to 2 K.

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Chapter 1

Climate Impact Research and Forest Management

1.1 Introduction

The fourth assessment report of the IPCC highlights significant climate change effects on natural systems in Europe (Parry et al., 2007). Particularly, the temperature increase induces forest-system-relevant changes in Europe. For instance earlier leaf-unfolding in spring, poleward and upward shifts of plant species ranges, and alterations in disturbance regimes of forests due to fires and pests have been observed (Lenoir et al., 2008; Menzel et al., 2001, 2008; Pucko et al., 2011; Walther et al., 2005). The measured overall warming for the Northern hemisphere between 1979 and 2005 has been 0.23-0.25 K per decade (Solomon et al., 2007). Also the precipitation pattern of Europe is affected by the climate warming. Projections of future climate change for Central Europe agree on a likely increase of winter and a decrease in summer precipitation accompanied by an increasing risk of summer

drought. However, there is still much uncertainty and variability in future climate trends, particularly in short-term climate projections of Central Europe (Solomon et al., 2007).

The recent climate of the North-eastern German lowlands after the Köppen-Classification is a cold climate without dry seasons and with warm summers (Peel et al., 2007). The macro climatic conditions of the federal state of Brandenburg is differentiated by the oceanic climate in the Northwest and the continental climate in the South. The long-term average annual temperature is between 8 and 9 °C and the average precipitation sum of a year add up to 450 – 660 mm. The average annual temperature in Germany has increased by circa 1.2 K since the beginning of the industrialization. In Brandenburg the warming trend is slightly smaller than the average of Germany and amounts to 0.95 K (DWD, 2012). The annual precipitation sum has increased by 4.3 % for the same period. However there are differences between winter and summer precipitation. Within the winter months (December-February) fell 21.1 % more precipitation but the summer months (June-August) experienced a decrease of 3.4 %. Under recent climate conditions there is already a low average precipitation sum in the growing season between 250 and 350 mm. This exacerbates the potential climate risk for managed natural systems which is characterised by two major changes, the increasing intensity of heavy rain events and the increasing duration of drought events (Holsten et al., 2009).

Landform configuration and soils have been established in Brandenburg mainly during the last glacial period. The forests grow on soils which sediments originate from end moraines, frontal plains and ground moraines. The differences in altitude are marginal, the highest peaks in Brandenburg are around 200 m over sea level. In the past century every site type in Brandenburg has been recorded by forest scientists

(Müller and Luthardt, 2009). Accordingly, 52 % of the soils have low nutrition contents and are characterized by low water holding capacities due to a high amount of sand (> 80 %). However, most of the soils are deeply penetrated by roots (> 1 m) and therefore the amount of plant available water is around 200 mm and 300 mm (Riek and Stähr, 2004).

In Brandenburg 36.5 % of the total area is covered by forests and it belongs to the five most densely forested federal states of Germany. Scots pine (*Pinus sylvestris* L.) is the dominant tree species with a share of 72 %. Other tree species with a relevant percentage of the tree species distribution are the broad-leaf tree species Sessile (*Quercus petraea* (Mattuschka) Liebl.) and Pedunculate Oak (*Quercus robur* L.), which sum up to 6 %, and European Beech (*Fagus sylvatica* L.) with 5 % (Müller and Luthardt, 2009). The average growing stock volume (over-bark) in Brandenburg is with 257 m³/ha at the lower end compared to the other federal states. Averaged over all age classes Scots pine and oak stands have 261 m³/ha and beech stands 377 m³/ha growing stock volume per hectare. The Scots pine stands are still mainly mono-specific and even-aged. Here the aim is to transform these forest stands into mixed and vertical diversely structured forest stands.

Higher temperature is linked to a higher evaporation demand of the atmosphere and could therefore aggravate water shortage especially in sandy forest soils. There is already a measured trend of decreasing available soil water on the whole forest area of Brandenburg (Holsten et al., 2009). Therefore climate change has become a major issue on the agenda of the long-term overall forest planning. Several activities were conducted which aim at the improvement of practical guidelines with respect to climate change (e.g. "Eberswalder Erklärung" (Spathelf et al., 2008), revision of silvicultural guidelines (Luthardt, 2006; Kölling and Ammer, 2006)). In addition,

strategies of forest transformation from even-aged mono-specific forest stands to diverse mixed forest stands are discussed as proactive adaptation options to climate change (Bolte et al., 2009; Jenssen, 2009). Originally, the idea of forest transformation was only based on forest related aspects. Economical and ecological concerns regarding the stability and ecological functioning of pure even-aged coniferous forest stands drive the discussion starting in the late 1980's (BMELF, 1994; Jenssen et al., 2006; Zerbe, 2002). Notably the climate warming of the last twenty years accompanied by extreme weather conditions (e.g. Elbe-flood 2002, summer drought 2003, numerous mild winter (DWD, 2012)) led to a shift of the forest transformation debate also towards aspects of climate change (Elmer et al., 2009a; Lasch et al., 2009a,b). Now forest transformation is not only an improvement of forest condition but also one necessary adaptation to climate change. This meaning is also underlined by the current general adaptation strategy to climate change of Germany.

”Aus waldbaulicher Sicht sollten möglichst stabile, gemischte Bestände angestrebt werden, die eine grössere Widerstandsfähigkeit gegen grossflächige Unglücksereignisse (Kalamitäten) durch beispielsweise Stürme und Borkenkäfer sowie ein grösseres Anpassungsvermögen an sich ändernde Klimabedingungen haben.” (BMUNR, 2008)

In Brandenburg the long-term overall forest planning of 1997 plans on 40% of the pure pine forest area a forest transformation with either oak or beech trees into mostly mixed pine forests (Müller and Luthardt, 2009). For this kind of forest a major aspect of possible climate change impacts is the occurrence of drought events, since drought very often induces a decline in the vitality of oak and pine trees. Hence, there is a great demand for research results which reduce the gap of

knowledge concerning adaptation potentials and climate change impacts of forest stands.

1.2 Climate Change Impacts on Scots Pine and Sessile Oak

After Hofmann and Pommer (2005) a large part of the southern and eastern forest area of Brandenburg would naturally be covered by mixed pine-oak, oak-hornbeam (*Carpinus betulus* L.) and pure pine forests. But as mentioned in the previous chapter, most of the forest area is stocked by pure Pine forests. Due to the economical and ecological disadvantages of this unbalanced tree species composition, some silvicultural and ecological experiments were conducted to get information about impacts of forest transformation. Several years ago experiments had started which analysed forest transformation processes with beech in pure pine forest stands in Brandenburg (Anders et al., 2005). Later also projects had been started which investigate Sessile and Penduculate oak as tree species for the transformation (Elmer et al., 2009c,a,b; Schröder et al., 2009). Generally, beech and oak are considered as the most important tree species for the transformation in Brandenburg.

Scots pine is a tree species with a very large distribution area across almost whole Europe until the east of Siberia in Asia. The core of its distribution is located in the boreal zone of evergreen forest. There are several subspecies of Scots pine which had to adapt to specific local growing conditions (Endtmann, 2007) which hamper general predictions of productivity changes due to climate change (Savolainen et al., 2011; Matias and Jump, 2012). The North-eastern lowlands of Germany and Brandenburg are located at the edge of Scots pine's natural distribution (EUFORGEN,

2009). However, there is a discussion how to evaluate the presence of Scots pine to the west of this frontier. Especially the stands under oceanic climate conditions of Belgium and France show the physiological adaptation potential besides the natural distribution. In last years the method of habitat modelling by using *climate envelope models (CEM)* has been applied to analyse the exposure to climate change. The range of the mean temperature of July within the current distribution is within 5 and 22 °C. The range of the mean temperature in January is within –25 and 5 °C and the precipitation sum of May-September is between 147 and 1044 mm.

The results of *CEM's* driven by climate scenarios indicate a high vulnerability of Scots pine to increasing temperatures in summer (Henschel, 2008). Under moderate climate change scenarios the CEM propose a disappearance of Scots pine in Germany (Kölling, 2007; Henschel, 2008). Scots pine is a tree species which is well adapted to water shortage and is competitive also on very dry sites in the North-eastern lowlands. Nevertheless pine stands react on severe droughts with growth reduction, increased needle fall and a higher exposition to damages by other biotic or abiotic factors (Beck, 2007; Möller et al., 2007; Wenk and Apel, 2007). These findings are in line with reported increasing mortality of Scots pine in the south-western frontier of the distribution (Rebetez and Dobbertin, 2004; Galiano et al., 2010; Poyatos et al., 2007; Gimmi et al., 2010).

Sessile oak is also a tree species which is adapted to a warm temperate climate and occasional drought events. The distribution stretches from the Mediterranean coastline across Central Europe to the South of Scandinavia. It is limited by the minimum temperature in winter which should not go below –20 °C. The results of the *CEM's* indicate climate ranges for the mean temperature in January between –14 and 9 °C. The mean temperature in July is between 7 and 28 °C and sum of pre-

precipitation from May to September is 62 – 830 mm (Henschel, 2008). Sessile oak is expected as one of the "winner" tree species under a warming climate in Germany and therefore an important tree species for forest adaptation and transformation (Kölling, 2007).

However, *CEM's* does not include the physiology of tree growing processes. From their statistical approach they have to assume climate causality for the current observation of Scots pine distribution which limits the explanatory power and therefore the predictive power for the future distribution (Ibanez et al., 2006). Another method studying climate impacts on tree growth and habitat suitability is to model the physiological response with process based modelling tools (Mäkelä et al., 2000; Johnsen et al., 2001). Here, the questions concerning future growth trends can be answered with focus on specific tree growth related processes. For instance, drought responses can be analysed by simulating the coupled water-carbon cycle within a forest stand. These model experiments help to detect specific weather conditions which lead to increasing or decreasing productivity.

Since the 1990s there is a general increase of mortality within oak stands in several regions of Germany. For instance the report on forest damage in Brandenburg indicates two different trends. While the crown transparency of pine trees features a clear improvement from 25 % of the 1990s to currently 10 %, the crown transparency of oak trees remains at a high level of currently 25 % (MIL, 2011). In addition, 20 % of oak trees are classified to the categories medium and strong biotic damages (MIL, 2011). Oak as a ring porous tree species is sensitive to summer drought. The water conductivity of a tree ring works in maximum 1.5 years. It means that only the two last tree rings serve as conduct for the transpiration water. If there is summer drought the water conducting tree ring exhibit missing vessels. This drop in con-

ductivity leads to a decrease in transpiration and consequently decreases the carbon assimilation of the tree (Kätzler et al., 2006). Experiments with young oak trees suggest strong impacts on the water balance if treated with a combination of defoliation and water stress. Particular the lower fine root biomass of defoliated trees causes lower water uptake capacities of oak trees during subsequent water stress periods (Gieger, 2002). The concurrence of different biotic and abiotic factors (see Fig. 1.1) further enhance the risk for a decrease of vitality in oak stands and is supported by other studies of north and central Europe (Jung et al., 2000; Thomas et al., 2002; Helama et al., 2009). Climate factors (i.e. summer drought, mild winter and late frost events) are expected to exacerbate the problem of the complex phenomenon of oak decline (see Fig. 1.1). Their prolonged changing in the future due to climate change aggravate predictions about the development of oak stands. Thus, there are strong concerns about the future vitality and the adaptation potential of oaks and as follows long-term forest transformation objectives are questioned (Luthardt, 2005). Accordingly, in last years a number of research projects came up to investigate silvicultural risks and potentials under climate change for the north eastern lowlands (e.g. Oakchain (Elmer et al., 2009c), Newalnet (UFZ, 2010)).

1.3 Modelling of Drought Stress

Besides the observed and projected trend of decreasing amount of summer rainfall there is still high uncertainty in future precipitation dynamics of central Europe (Murphy, 2000; Ruosteenoja et al., 2006; Raisanen et al., 2004). However, in a warming climate the higher average temperature determines a higher evaporation

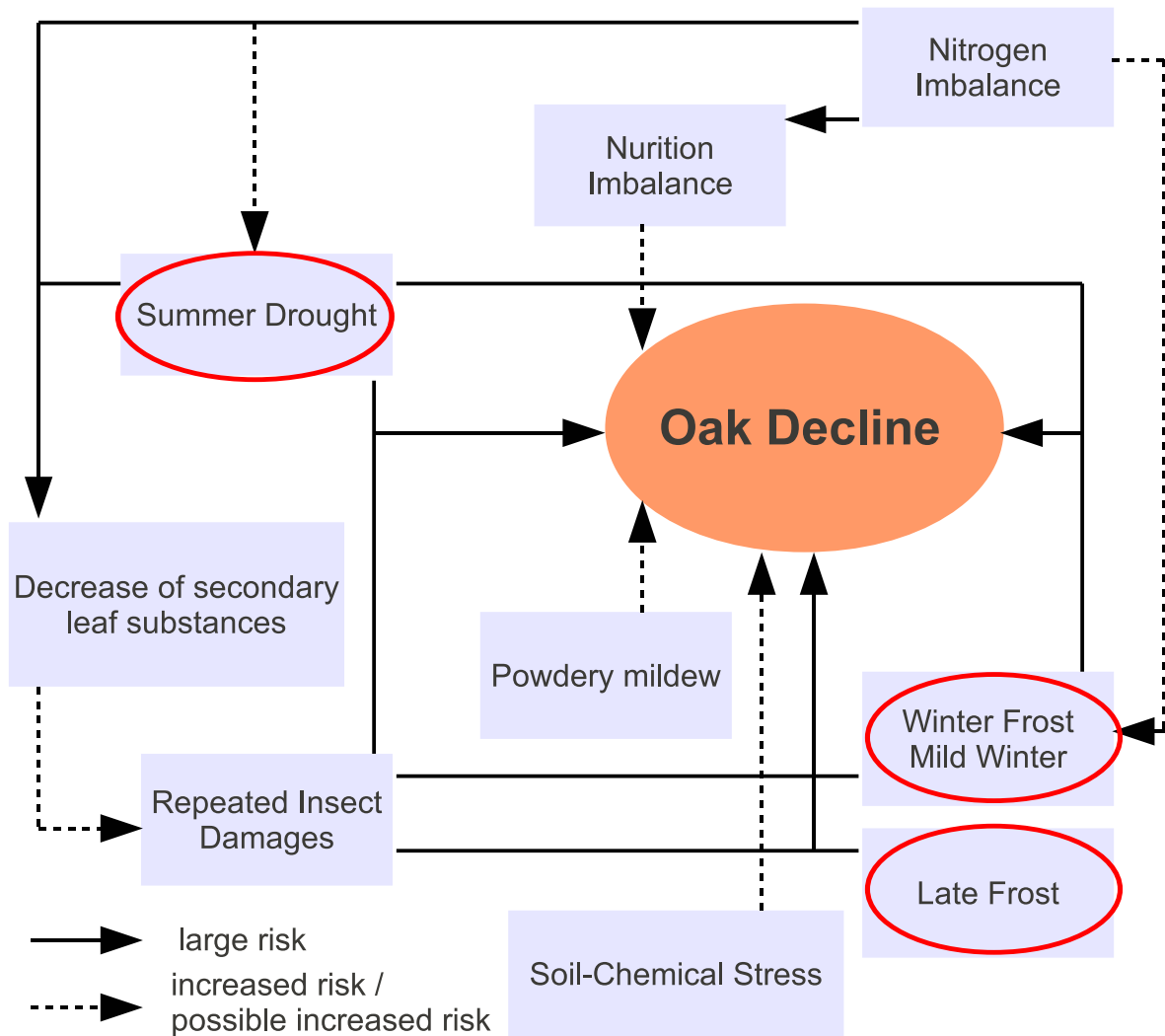


Figure 1.1: Scheme with interaction of main factors for vitality loss of oak stands with emphasis of the red-framed climate factors. (modified from (Kätzel et al., 2006)).

demand of the atmosphere. This alone could aggravate water shortage in forest soils. Conversely there is a measured increase of water use efficiency of temperate forests which should persist with increasing amount of atmospheric CO₂ (Arneth et al., 2002; Duquesnay et al., 1998; Feng, 1999). The increasing water use efficiency

based on the increased uptake of CO₂ as a result of its higher concentration in the atmosphere at the same transpiration level. Centritto et al. (2002) showed large effects of increased water use efficiency (up to 63 %) of saplings (*Prunus persica* (L.) Batsch) at higher CO₂ concentrations (700 versus 350 μmol·m⁻¹). Broadmeadow and Jackson (2000) also found increased water use efficiency at saplings of *Quercus petraea* and *Pinus sylvestris*. They concluded a higher potential for young trees to survive drought events. On the other hand they pointed out that it could likely to be counterbalanced by an increase in LAI (leaf area index) and, hence, increasing water loss on a ground area basis. There are still huge knowledge gaps concerning plant responses to combinations of changing factors as water availability, warming and CO₂ concentration. To complicate matters further, most of the experimental results are hardly transferable on mature natural forest stands (Körner, 2006; Norby et al., 2010; Norby and Zak, 2011).

Severe droughts decline the productivity of forests. Detailed investigations of effects of the European heat wave in summer 2003 explained low forest productivity with the water shortage in soils. Particular beech stands indicated declining productivity in the following year (Granier et al., 2007). Generally, in central Europe there is a correlation between the available water within the growing period and the growth of mature forest stands (Breda et al., 2006). The annual radial increment of a tree is a suitable measure for its productivity. Hence, the analyses of tree rings by tree core samples or trunk discs is a good method to detect water stress of trees, especially for periods in the past (Beck, 2009). Analyses of oak stands in the west of Germany showed a close relationship of the *Palmer Drought Severity Index (PDSI)* and the index of annual radial increment (Friedrichs et al., 2009). The physiological reason for this relationship bases on the trade-off between cavitation (lost of conductivity

in vessels of roots and stem) and photosynthetic activity and resulting gas exchange of leaves (Maherali et al., 2006). Among the tree species there are different strategies how to arrange this trade-off. They can be classified into two groups: *i*) Tree species, which are at low risk of cavitation and sustain water flow at low water potentials. *ii*) Tree species, which reduce transpiration at comparable high water potentials to avoid cavitation in root and stem vessels (Cruiziat et al., 2002).

The realistic calculation of the amount of supplied water by roots is a crucial feature of a forest growth model to estimate water stress. For the calculation exist two different general approaches. The first, it can be calculated by an empirical function dependent on soil water content (e.g. (Chen, 1993)). The second, a physical representation of water flow within the tree by deterministic models. For the latter a number of models, which have a different grade of complexity, has been developed (Cowan, 1965; Lang et al., 1969; Hunt et al., 1991; Cruiziat et al., 2002). The prevailing models describe the soil-plant-atmosphere continuum as an electrical circuit with resistances (water conductivity of soil, root, stem and leaf) and capacitance (water stored in the stem). These models consists of ordinary differential equations with empirical derivable parameters (Campbell, 1991; Williams et al., 1996; Chuang et al., 2006). They simplify the spatial-temporal dynamics of the water transport within trees and can be integrated in physiological based forest growth models (Williams et al., 2001a,b).

1.4 Forest Decision Making under Uncertainty

Exact predictions of future developments as for example for climate, timber demand or socioeconomic development are impossible. However these developments set the

basic conditions of forest related decision making processes. Decisions of today inevitably has to be made under uncertain assumptions of the future development (Ananda and Herath, 2009). In addition, forests supply a number of ecosystem goods and services and are committed to a variety of requirements (Borchers, 2010). On the majority of forest area of Brandenburg the objective is the synchronous management of divers forest functions (e.g. habitat and species conservation, timber supply, water conservation, carbon sequestration). This can lead to conflicts due to opposed interests or objectives and their required different management strategies. Forest management strategies has to consider and increase adaptation potentials of forest systems to establish stable forest stands which management objectives under (Bolte et al., 2009; Reyer et al., 2012). Finally, every management strategy and objective has to be reconsidered regularly due to new knowledge or changing basic site conditions. For this ongoing assessment of strategies, concepts and methods are needed to quantify their impacts and suitability to achieve objectives.

The definition of different scenarios and the investigation of their impacts with the help of mathematical or conceptual models is one general approach to analyse potential future developments (Chermack et al., 2001; Chermack, 2004). Decision-making to achieve different objectives is accompanied by several uncertainties. On the one hand, there is the uncertainty about the future climate development and its subsequent impacts. This results in uncertainty about the suitability of management strategies to achieve the specified objectives. On the other hand, there are model uncertainties inherent to model processes and defined parameter values (Saltelli et al., 1999). This, in turn, also affects the uncertainty of simulated climate impacts. Therefore, a good strategy accounting for climate uncertainty should include a calculation of a performance measure which gives probabilities to max-

imize multi-criteria objectives and minimizing risks for failure (Yousefpour et al., 2012). Since climate change do not only affect the mean level but also the variance of forest productivity, the applied approach should account for these two aspects. So far, indices (e.g. option value, stochastic dominance) dealing with uncertainty have been developed for forest management-related decision-making (Jacobsen and Thorsen, 2003; Prato, 2008a). Such approaches support the decision-making process to handle future uncertainties and risks.

1.5 Research objectives

The main emphasis of the work is to provide model based analysis of growth and development of forest stands relevant for the federal state of Brandenburg. Using physiological based forest growth models and climate scenarios allow the estimation of the future state of forest stands and the evaluation of potential risks. The focus of the work is on mixed oak-pine forests which are planned for the continental and drier regions of Brandenburg. The studies presented here are conducted with the physiological based forest growth model *4C-FORESEE* (Lasch et al., 2005).

The first research objective of this work focuses on productivity of four main tree species (*Quercus robur* and *petraea*, *Fagus sylvatica*, *Pinus sylvestris*, *Picea abies* (L.) H.Karst.) in whole Germany under several climate change scenarios. A statistical approach is introduced which allows an estimation of the average annual net primary production (NPP) depending on three climate and two soil variables. This method makes a quick and efficient spatial dependent characterisation of climate scenario impacts possible and is the base for an assessment which regions and tree species are mostly affected in Germany. Following specific questions will be answered:

- How does the NPP for the four main tree species of Germany depend on climate factors?
- What are the impacts of climate change on NPP of the four tree species ?
- Which regions in Germany are likely to experience a significant change in NPP?
- How large is the uncertainty of NPP regarding climate scenarios and are there regional differences?

The second research objective is the comparison of two different model approaches of water uptake by roots with respect to tree growth. This results in an evaluation of their capability to simulate drought stress. The questions for this work are:

- What are the effects of using two different water uptake approaches in *4C* on model behaviour?
- How do simulated results of transpiration and annual diameter increment fit to measured data?
- Is the forest growth model *4C* able to describe with both water uptake approaches the impacts of extreme weather events like droughts on diameter increment?

The incorporation uncertain effects and developments within decision processes of forest management related issues is the focus of the third research objective. The impact of different climate scenarios and different management strategies on a specific forest stand, representative for the forest transformation, is discussed. The interaction between impacts are investigated and assessed with regard to different

management objectives for this stand. This allows an integrated impact study of factors discussed in previous chapters (e.g. productivity, drought risks) and results in the quantification of climate scenario uncertainty and the uncertainty which comes from management effects. This lead to the questions:

- What are the contributions of management and climate scenario effects on the uncertainty of future forest production in mixed oak-pine forest stands?
- Is it possible to apply a general evaluation criteria from literature on a specific forest stand which is representative for the forest transformation in Brandenburg?

1.6 Structure and Co-Worker of the Thesis

- *Chapter 2* introduces the main methods used in this work. At first the process based forest growth model *4C* is explained. Second, the two different water uptake approaches will be described in detail. Third the characteristics and the source of the applied climate scenarios are presented.
- The content of *chapter 3* based on the original paper *Evaluating the productivity of four main tree species in Germany under climate change with static reduced models. Annals of Forest Science, 2016, volume 73, issue 2, pp 401-410*. The share of my contribution to this study were the the general idea to use a reduced model to estimate the NPP change, execution of the simulation, the formulation of the polynomial function. The support of the other authors *Petra Lasch-Born, Felicitas Suckow, Christopher P.O. Reyer* consisted on the help in writing the publication an discussing the results.

- The content of *Chapter 4* has been published under the title "*Modeling of Two Different Water Uptake Approaches for Mono- and Mixed-Species Forest Stands*" in *Forests*, 2015, volume 6, issue 6, pp 2125-2147 and shows the analysis of two different water uptake approaches to model oak and pine tree growth in a mixed stand. I implemented the model formulation in the source code of *4C* and conducted the model study. The listed other authors *Petra Lasch-Born*, *Felicitas Suckow*, *Christopher P.O. Reyer* formulated the idea of comparing an alternative water uptake model and supported the writing of the publication.
- *Chapter 5* illustrates the assessment of different forest management strategies under the uncertainty of climate change scenarios. The simulation study were presented at the conference "*Mixed Forest in a Changing World*" and has been published by the journal *Forest Systems*, 2011, volume 20, issue 3, pp 453-463, "*Management of mixed oak-pine forests under climate scenario uncertainty*". The idea and work was done by myself with support of the co-authors *Petra Lasch*, *Felicitas Suckow*, *Christopher P.O. Reyer* with discussion and writing.
- *Chapter 6* gives a comprehensive discussion of the specific result of chapters 3 to 5.
- *Chapter 7* draws an overall conclusion of the specific result chapters 3 to 5 and of general findings concerning impacts and vulnerabilities to mixed oak-pine forests in the North-eastern lowlands.

Chapter 2

Methods

My thesis uses modelling techniques to handle ecological processes which are changing over a long time period. It is necessary to revert to forest growth models due to a lack of experiments which can cover the large variety of possible future climate change and their impacts on forest ecosystems. I used the process-based forest growth model *4C*, because it provides some key features which make it very beneficial for my thesis work. First of all, it is climate sensitive. The main driver of forest growth is the weather at a daily time step. Also it contains a coupled soil-plant-atmosphere system which allows me to simulate changing site conditions and their effects on the water flow within this system. It is a stand-based model and calculates all relevant material flows of a forest stand which I need to evaluate different management strategies. Finally, it is well established and validated, for instance, within the EU-project *SILVISTRAT* (Fürstenau, 2008).

2.1 The Forest Growth Model 4C

2.1.1 General Description

The forest growth model 4C (*FORESt Ecosystems in a changing Environment*) acts on an approach which describes plant growth as functional relationships between physiological processes and environmental factors (Lasch et al., 2005). The relationships based on physiological experiments and long-term observed forest stand data (Haxeltine and Prentice, 1996). It has been developed to simulate forest stands with high temporal and spatial resolution. Establishment, growth, and mortality are explicitly modelled on individual patches for which homogeneity is assumed. The model simulates tree species composition, forest structure, leaf area index as well as ecosystem carbon and water balances. The simulated stand is divided into different cohorts of trees. One cohort consists of trees of the same tree species and trees have equal dimensions of tree height and tree diameter. The cohort structure of simulated tree growth enables a detailed analysis from stand to single-tree level. The model has been used to simulate growth, water, and carbon budget of trees and soils under current and projected climate condition and to analyse the long-term growth behaviour of forest stands with different tree species. 4C was applied in different studies and validated across a wide range of forest sites (Bugmann et al., 1997; Lasch et al., 2005, 2002b). In the current version of the model following tree species are parametrized: beech (*Fagus sylvatica L.*), spruce (*Picea abies L. Karst.*), Scots pine (*Pinus sylvestris L.*), oak (*Quercus robur L. and Quercus petraea Liebl.*), birch (*Betula pendula Roth*), poplar (*Populus tremula (L.), P. tremuloides (Michx.)*), Aleppo pine (*Pinus halepensis Mill.*), Ponderosa pine (*Pinus ponderosa Dougl.*), Black locust (*Robinia pseudoacacia L.*) and Douglas fir (*Pseudotsuga men-*

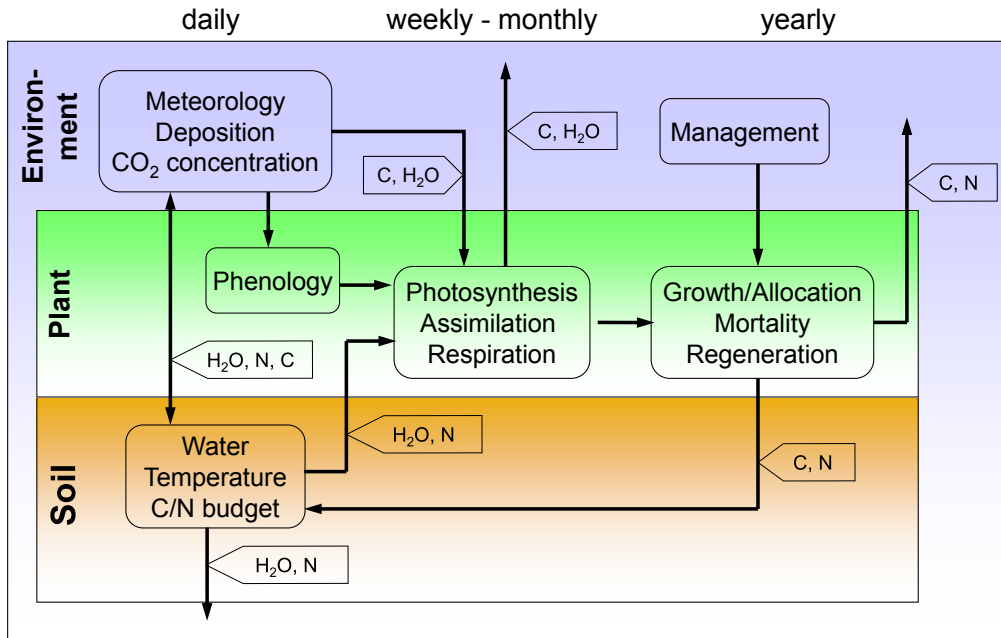


Figure 2.1: Model scheme - overview of principle interactions of the sub-models (Lasch et al., 2002a)

ziesii (Mirbel) Franco).

The model contains different sub-models which simulates the different processes at different time scales (Fig. 2.1). Daily weather data are used as input data to calculate soil water and temperature dynamics and to calculate the length of the growing season. The length of the growing season is provided by a species-specific phenological model with prohibitors and inhibitors which are dependent on air temperature and day length (Schaber and Badeck, 2003). The daily transport of heat and water in a multi-layered soil is explicitly calculated, as well as carbon and nitrogen dynamics based on the decomposition and mineralisation of organic matter. Water balances are calculated using a bucket model approach (Glugla, 1969; Koitzsch, 1977). The

soil column is divided into different layers with optional thickness according to the horizons of the soil profile. Each layer, the humus layer and the deeper mineral layers, is considered homogeneous concerning its physical and chemical parameters. Water content and soil temperature of each soil layer are estimated as functions of the soil parameters, air temperature, and stand precipitation and control the decomposition and mineralization of organic matter. The water input to the soil is equivalent to the throughfall (precipitation minus interception). The interception is determined by the interception storage and the potential evapotranspiration. The interception storage is calculated from a leaf area index that is weighted by a species specific storage capacity (Grote and Suckow, 1998).

The photosynthesis sub-model is calculated at a 7-day time step. The model is described under the assumption of unlimited water and nutrient supply. The annual course of net photosynthesis is simulated with a mechanistic formulation of net photosynthesis as a function of environmental influences (temperature, water and nitrogen availability, radiation, and CO₂) where the physiological capacity (maximal carboxylation rate) is calculated based on optimisation theory after Haxeltine and Prentice (1996). The calculation of total tree respiration following the concept of constant annual respiration fraction as proposed by Landsberg and Waring (1997). The explicit simulation of water and nutrient availability as perceived by individual trees leads to a reduction of the maximum photosynthesis described before. For both the nitrogen and the water availability a reduction of photosynthesis is calculated based on the ratio between supply and demand.

At a yearly time step allocation of carbon, tree growth, mortality and management take place. The allocation pattern of annual NPP are modelled with a combination of pipe model theory (Shinozaki et al., 1964), the functional balance hy-

pothesis (Davidson, 1969) and allometric relationships which are affected by water and nutrient limitations. Mortality can be caused either by stress due to negative leaf mass increment in successive stress years or by an intrinsic age-dependent and generic component (Loehle and LeBlanc, 1996). Management actions as thinning and planting can be applied and are simulated once at the end of the simulation year. In the following subsections modelling approaches which are relevant for my work are introduced in particular.

2.1.2 *4C*-Simulated Water Flow in Forest Stands

An important issue is the analyses of tree drought stress. In chapter 4 the application of two different water uptake approaches are compared. Within the model *4C* a number of processes are simulated with direct link to water uptake by roots and transpiration of leaves. First the potential evapotranspiration is calculated. Several methods exist (McKenney and Rosenberg, 1993) and the most important are implemented in *4C*. The amount of potential evapotranspiration is reduced by simulated soil evaporation and intercepted water to get the amount of water which is potentially transpired by the vegetation of the stand. With the help of the potential transpiration the actual transpiration is calculated dependent on the photosynthetic activity. The result is a cohort-specific transpiration demand. Dependent on the root distribution within the soil and soil water content the water supply by roots is simulated. The daily derived ratio $\frac{W_S}{W_D}$ between water supply W_S and water demand W_D is averaged over the whole year and reduces the sum of NPP at the end of the year.

Potential Evapotranspiration

For Germany the simple approach by *TURC-IVANOV* is suitable for most regions and therefore also used in this work. The potential evapotranspiration is calculated on two ways depending on the air temperature (DVWK, 1996): at $T_a \geq 5^\circ\text{C}$ it is calculated from air temperature T_a and global radiation R_g by an equation of *TURC*:

$$E_{pot} = 0.0031 \cdot f_{korr} \cdot (R_g + 209) \cdot \frac{T_a}{(T_a + 15)} \quad (2.1)$$

The modification factor f_{korr} depends on the relative humidity h_r :

$$f_{kor} = \begin{cases} 1 + \frac{50-h_r}{70} & , h_r < 50 \\ 1 & , h_r \geq 50 \end{cases} \quad (2.2)$$

If air temperature is $T_a < 5^\circ\text{C}$ then the equation proposed by *IVANOV* is used:

$$E_{pot} = 3.6 \cdot 10^{-4} \cdot (100 - h_r) \cdot (T_a + 25) \quad (2.3)$$

Interception

The interception rate S_{int} is calculated by an approach suggested by Jansson (1998). Here interception is defined as the amount of precipitation which is evaporated by trees and soil vegetation and does not come to the soil. The interception capacity S_{imax} is dependent on the vegetation canopy which is a function of the leaf area index LAI and the species specific parameter i_{LAI} :

$$S_{imax} = i_{LAI} \cdot LAI \quad (2.4)$$

with the interception capacity of the vegetation, the interception rate S_{int} at time t is then:

$$S_{int}(t) = \min [P(t), (S_{i_{max}} - S_i(t - 1))] \quad (2.5)$$

where P is precipitation and $S_i(t - 1)$ is the interception storage remaining from the previous time step.

Soil Evaporation

Potential soil evaporation E_{soil} is calculated with the potential evapotranspiration (E_{pot}) from equation 2.1-2.3. Similar to approaches as for example Ritchie (1972) the potential soil evaporation is limited by shading of the vegetation:

$$E_{soil} = E_{pot} \cdot \exp(-0.6 \cdot LAI) \quad (2.6)$$

This potential soil evaporation demand (Fig. 2.2) is captured by the soil water up to a certain soil depth.

Soil Bucket Model

The soil water module is based on a storage approach proposed by Glugla (1969). The soil is divided into any number of layers according to the soil survey and its soil horizons. The parametrization of the layers includes variables like thickness, texture, porosity, stone content, bulk density, permanent wilting point and field capacity. The inflow of water into one soil layer results from percolation of the above soil layer W_p . The first soil layer receives the throughfall (stand precipitation minus canopy interception). The outflow of water is the sum of evaporated water W_{ev} (up to a certain soil depth), water uptake by roots W_{upt} and percolation water

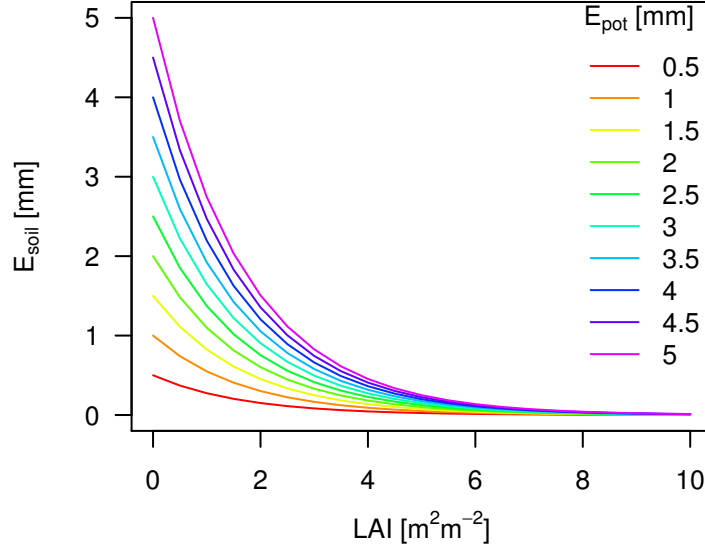


Figure 2.2: Relationship between daily potential soil evaporation (E_{soil}), leaf area index (LAI), and potential evapotranspiration (E_{pot}) within 4C.

($W_s(t) - W_s^{FC}$), where W_s is the soil water content and W_s^{FC} is the soil water content at field capacity. Velocity and amount of percolation water is controlled by the soil texture depending parameter λ_W (Glugla, 1969; Koitzsch, 1977):

$$\frac{d}{dt} (W_s(t) - W_s^{FC}) = W_p(t) - W_{upt}(t) - W_{ev}(t) - \lambda_W \cdot (W_s(t) - W_s^{FC}) \quad (2.7)$$

Root Distribution

The distribution of fine root biomass is calculated after an empirical function derived by Jackson et al. (1996). The function proposes an asymptotic increase of cumulative fine root biomass fraction Y with soil depth d (Fig. 2.3 and equation 2.8).

$$Y = 1 - \beta^d \quad (2.8)$$

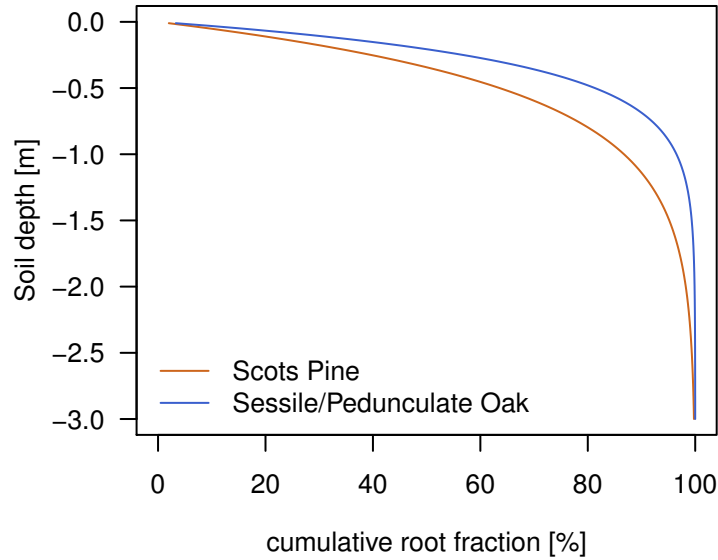


Figure 2.3: Relationship between fine root biomass and soil depth after Jackson et al. (1996)

They investigated a global distribution dataset and fitted the function to different vegetation types. Hereafter, the "extinction coefficient" β for temperate coniferous forests is around 0.98 and for temperate deciduous forest is around 0.967. Hence, more fine roots are distributed in the upper soil layers for Oak than for Scots pine (Fig. 2.3).

2.2 Modelling Root Water Uptake

Two different root water uptake approaches has been analyzed. The first one ($WU1$) assumes an optimal water uptake by roots at $\pm 10\%$ of soil field capacity. If soil water content below or above this threshold the amount of water uptake is linear decreased. The second one ($WU2$) represents the water uptake by roots along the soil-plant-atmosphere-continuum ($SPAC$) similar to the electrical circuit. The water follows

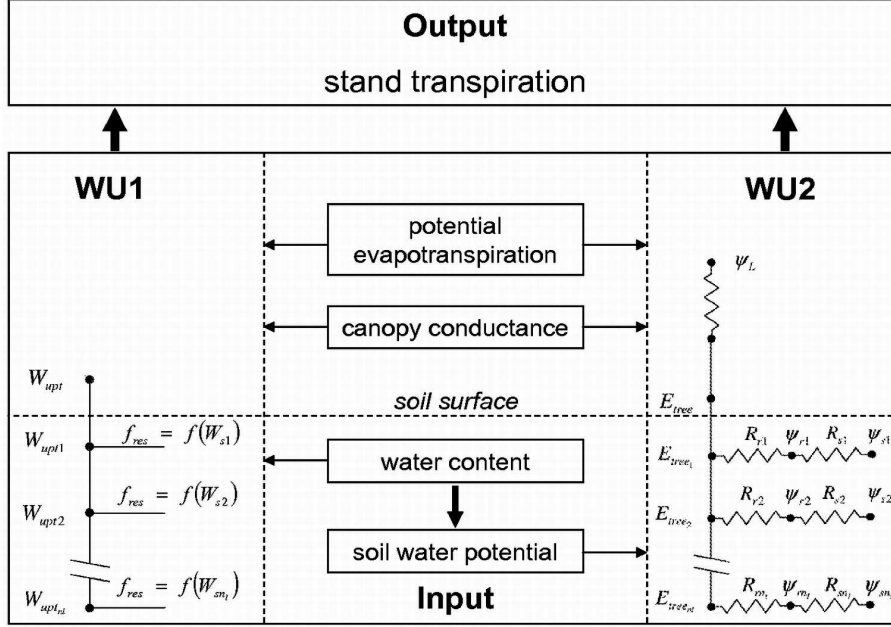


Figure 2.4: Overview of the two water uptake approaches with the considered model components. With W_{upt} and E_{tree} = sum of water uptake of a tree over n_l number of soil layers, W_s = soil water content, R_r = root resistance, R_s = soil resistance, ψ_L = leaf water potential, ψ_r = root water potential, ψ_s = soil water potential.

the water potential gradient within the continuum. Important components of the *SPAC* as resistances (R), water potentials (ψ) and water fluxes (E) are calculated for different parts (e.g. soil, roots, leaves) of the continuum. The following figure show the modelled parameter of both water uptake approaches (see Fig. 2.4).

2.2.1 Calculation of Transpiration Demand

The transpiration demand of a tree cohort (D_{tr}^c) is calculated in the same way for both analysed water uptake approaches WU1 and WU2. At first the potential evapotranspiration (E_{pot}) is estimated by the method of *Turc/Ivanov* (DVWK, 1996).

The potential stand transpiration (D_{tr}) results from interception (E_{int}), soil evaporation (E_{soil}), the total canopy conductance (g_{tot}), the assumed maximum total canopy conductance (g_{max}) ($= 14000 \text{ mol m}^{-2} \text{ day}^{-1}$) and an empirical parameter ($\alpha_m = 1.4$, the maximum Priestley-Taylor coefficient (Monteith, 1995)):

$$D_{tr} = (E_{pot} - E_{int} - E_{soil}) \cdot \alpha_m \cdot \left[1 - e^{\left(\frac{-g_{tot}}{g_{max}}\right)} \right] \quad (2.9)$$

The total canopy conductance (g_{tot}) is determined by the sum of unstressed stomatal conductance of all trees and the total soil vegetation. The unstressed stomatal conductance (g_{ptree}) of one *tree* within a cohort c and the total soil vegetation, respectively, is dependent of the assimilation rate (A_{dtree}) of the tree and the atmospheric carbon dioxide content (c_{co2}):

$$g_{tot} = \sum_{tree=1}^{N_{tree}} g_{ptree} \quad (2.10)$$

with

$$g_{ptree} = \max \left[0, \frac{1.56 \cdot A_{dtree}}{(1 - \lambda) \cdot c_{co2} \cdot C_{mass}} \right] \quad (2.11)$$

where C_{mass} is molar mass of carbon and N_{tree} is number of trees in the stand. The ratio of the total potential stand transpiration (D_{tr}) to the total stand canopy conductance (g_{tot}) is used to calculate the transpiration demand of a tree cohort (D_{tr}^c):

$$D_{tr}^c = g_{ptree} \cdot N_{tree}^c \cdot h_{dem} \quad (2.12)$$

with

$$h_{dem} = \frac{D_{tr}}{g_{tot}}$$

where N_{tree}^c is the number of trees in a cohort.

2.2.2 Water Uptake Approach WU1

This water uptake approach was originally proposed by Chen (1993). The water is extracted from soil layers, starting in the upper layer, regarding the cohort-separated transpiration demand (D_{tr}^c). The water supply by roots (W_{upt}^c) is calculated by WU1 as follows:

$$W_{upt}^c = W_s \cdot f_{res} \quad (2.13)$$

where W_s is the soil water content [mm].

The reduction factor (f_{res}) which implies the reduced water uptake at water contents besides the optimum is simulated as follows:

$$f_{res} = \begin{cases} 1 - \frac{0.9 \cdot W_s^{FC} - W_s}{0.9 \cdot W_s^{FC} - W_s^{WP}} & , W_s < 0.9 \cdot W_s^{FC} \\ 0.3 + 0.7 \cdot \frac{W_s^{sat} - W_s}{W_s^{sat} - 1.1 \cdot W_s^{FC}} & , W_s > 1.1 \cdot W_s^{FC} \\ 1 & , \text{otherwise} \end{cases} \quad (2.14)$$

where W_s^{sat} is the saturated water content of soil layer, W_s^{FC} is the soil water content at field capacity and W_s^{WP} is the soil water content at wilting point.

2.2.3 Water Uptake Approach WU2

WU2 calculates the water supply of the roots W_{upt}^c for cohort c with water content of the soil W_s and transpiration of one tree from cohort c :

$$W_{upt}^c = \min(N_{tree}^c \cdot E_{tree}, W_s) \quad (2.15)$$

where E_{tree} is the transpiration flow within the soil-plant-atmosphere continuum and is described analogous to Ohm's law in an electrical system. The transpiration is driven by the gradient between the water potentials of soil and leaf and reduced by the total resistance along the pathway. The following equations to calculate the transpiration rate and so the water uptake by roots were developed by Campbell (1991).

$$E_{tree} = \frac{(\psi_s - \psi_L)}{R} \quad (2.16)$$

where ψ_s is the soil water potential, ψ_L is the leaf water potential and R is the total resistance along the soil-plant-atmosphere continuum.

In this approach two single resistances were explicit modelled, the root endodermis resistance R_{ri} and the soil resistance R_{si} in a soil layer i . R_{ri} is directly proportional to the total root resistance R_r^{tot} and inversely proportional to the fraction of fine root length L_i in that layer:

$$R_{ri} = \frac{R_r^{tot} \cdot \sum_{i=1}^{n_l} L_i}{L_i} \quad (2.17)$$

where n_l is number of soil layers.

The required root length density L_i was estimated from species specific root length l_{SRL} , the fine root biomass in a soil layer M_{ri} calculated with a yearly time step, and the cylindrical rooted soil volume V_{root_i} :

$$L_i = \frac{M_{ri} \cdot l_{SRL}}{V_{root_i}} \quad (2.18)$$

To calculate V_{root_i} we use results of the investigation in a Norway spruce stand by (Ammer and Wagner, 2005) who assume a cylindrical rooted soil volume V_{root_i} with

the radius of horizontal root spread d_r (dependent on diameter at breast height d_{bh}) and the thickness of the soil layer Δz_i :

$$V_{root_i} = \pi \cdot d_r^2 \cdot \Delta z_i \quad (2.19)$$

with

$$d_r = \frac{d_{bh} \cdot 100}{6}$$

The soil resistance in a layer R_{si} is determined by the conductivity k_{si} , the fine root length density L_i and the water uptake E_{tree} . The rate of water uptake by a single root is described by following differential equation:

$$\frac{q}{A} = -k \cdot \frac{d\psi}{dr} \quad (2.20)$$

where q is the rate of water uptake by a root, A is root surface area, k is unsaturated hydraulic conductivity, ψ is the matrix potential and r the root radius. The root surface area A is:

$$A = 2 \cdot \pi \cdot r \cdot l \quad (2.21)$$

where l is length of the root.

The unsaturated hydraulic conductivity k is explained by:

$$k = k_{sat} \cdot \left(\frac{\psi_e}{\psi} \right)^n \quad (2.22)$$

where ψ_e is the air entry potential, k_{sat} the saturated hydraulic conductivity, and n a soil texture dependent constant.

Applying 2.21 and 2.22 in 2.20 and by integration from a point r_s , which represents

the average distance between two neighbouring roots and has the potential ψ_s , to root surface r_r , where the potential is ψ_r , one receives:

$$\left(\frac{q}{2 \cdot \pi \cdot l}\right) \ln\left(\frac{r_r}{r_s}\right) = \frac{(k_s \cdot \psi_s - k_r \cdot \psi_r)}{(1 - n)} \quad (2.23)$$

where k_r is hydraulic conductivity at the root surface and k_s is hydraulic conductivity of the soil.

The water uptake per unit root length q is related to root length density, soil depth and water uptake of the tree E_{tree_i} , if q is proportional to E_{tree_i} in a soil layer i with a specific root length density L_i and the thickness of the soil layer Δz_i :

$$\frac{q}{l} = \frac{E_{tree_i}}{L_i \cdot \Delta z_i} \quad (2.24)$$

The average distance between the fine roots is given by:

$$r_s = (\pi \cdot L_i)^{-\frac{1}{2}} \quad (2.25)$$

from 2.23, 2.24 and 2.25 by solving for water uptake E_{tree_i} we get the water uptake in layer i .

$$E_{tree_i} = \frac{(k_{ri} \cdot \psi_{ri} - k_{si} \cdot \psi_{si})}{B_i} \quad (2.26)$$

where

$$B_i = \frac{(1 - n) \cdot \ln(\pi \cdot r_r^2 \cdot L_i)}{(4 \cdot \pi \cdot L_i \cdot \Delta z_i)}$$

The soil resistance towards the water uptake following the electrical analogue is:

$$R_{si} = \frac{(\psi_{si} - \psi_{ri})}{E_{tree_i}} \quad (2.27)$$

where ψ_{ri} is the water potential in the root endodermis, and with the use of equation 2.26 follows:

$$R_{si} = \frac{B_i \cdot (\psi_{si} - \psi_{ri})}{(k_{ri} \cdot \psi_{ri} - k_{si} \cdot \psi_{si})} \quad (2.28)$$

The transpiration or water uptake of a tree is calculated with:

$$E_{tree} = \sum_{i=1}^{n_l} \frac{(\psi_{si} - \psi_{xri})}{(R_{si} + R_{ri})} \quad (2.29)$$

Assuming that axial resistances within the roots could be neglected then equation 2.29 can be solved for the water potential in the root xylem ψ_{xr} :

$$\psi_{xr} = \frac{\left\{ -E_{tree} + \sum_{i=1}^{n_l} \left[\frac{\psi_{si}}{(R_{si} + R_{ri})} \right] \right\}}{\sum_{i=1}^{n_l} \left[\frac{1}{(R_{si} + R_{ri})} \right]} \quad (2.30)$$

The leaf water potential ψ_L is given by:

$$\psi_L = \psi_{xr} - E_{tree} \cdot R_L \quad (2.31)$$

where R_L is the leaf resistance.

Equation 2.30 is implemented for ψ_{xr} in equation 2.31 and the result can be used to

calculate the leaf water potential:

$$\psi_L = \frac{\sum_{i=1}^{n_l} \left[\frac{\psi_{si}}{(R_{si} + R_{ri})} \right]}{\sum_{i=1}^{n_l} \left[\frac{1}{(R_{si} + R_{ri})} \right]} - \frac{E_{tree}}{\sum_{i=1}^{n_l} \left[\frac{1}{(R_{si} + R_{ri})} \right]} - E_{tree} \cdot R_L \quad (2.32)$$

The first term on the right side of equation 2.32 describes a weighted mean of the water potential because if one sets transpiration $E_{tree} = 0$ then becomes $\psi_L = \overline{\psi_s}$. The second term is the transpiration multiplied by a weighted mean of the root-soil-resistance $\overline{R_{sr}}$. Equation 2.32 has to be calculated simultaneously with equation 2.33 that describes the effect of the leaf water potential on the tree transpiration demand D_{tr}^{tree} .

$$E_{tree} = \frac{D_{tr}^{tree}}{\left[1 + \left(\frac{\psi_L}{\psi_c} \right)^a \right]} \quad (2.33)$$

where parameter a is equal to 10 and parameter ψ_c is the critical leaf water potential where $E_{tree} = \frac{D_{tr}^{tree}}{2}$.

Adaptation of WU2 for numerical implementation in 4C

The soil resistance of a soil layer R_{si} is a nonlinear function of water potential ψ_{ri} at the root surface which in turn is dependent on the water uptake E_{tree_i} (equation 2.28). An iterative method could be used to calculate the required potentials and resistances, but such an approach is very computational time consuming. Therefore an approximated soil resistance is used that is calculated once per day for every soil layer by simplification of equation 2.28 to:

$$R_{si} = \frac{B_i}{k_i} \quad (2.34)$$

Unit conversion of total root resistance for comparison

Campbell (1991) used for total root resistance the unit $[m^4 \cdot s^{-1} \cdot kg^{-1}]$ which is derived from equation 2.16. If $R = R_s + R_r^{tot}$ and $R_s = 0$, equation 2.16 is solved for R_r^{tot} . The units are as follows:

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [J \cdot kg^{-1} / kg \cdot m^{-2} \cdot s^{-1}]$$

$$\text{with } [J] = [kg \cdot m^2 \cdot s^{-2}]$$

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [kg \cdot m^2 \cdot s^{-2} \cdot kg^{-1} / kg \cdot m^{-2} \cdot s^{-1}]$$

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [m^4 \cdot s^{-1} / kg] = [m^4 \cdot s^{-1} \cdot kg^{-1}]$$

$$\text{with } [J \cdot kg^{-1}] = [kPa]$$

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [kPa / kg \cdot m^{-2} \cdot s^{-1}] |kg(water) \rightarrow m^3(water)| \cdot 10^3$$

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [kPa / m^3 \cdot m^{-2} \cdot s^{-1}] |kPa \rightarrow MPa| \cdot 10^{-3}$$

$$[m^4 \cdot s^{-1} \cdot kg^{-1}] = [MPa \cdot s \cdot m^{-1}]$$

The chosen unit for comparison is $[MPa \cdot s \cdot m^{-1}]$. Williams et al. (2001a) set the root resistivity in their simulation experiment at $100[MPa \cdot s \cdot g \cdot mmol^{-1}]$. Coners and Leuschner (2005) derived with sap flow gauges the water absorption per unit root surface area for three temperate tree species. They found root resistances per unit root surface between $2.6 \cdot 10^7$ and $1.25 \cdot 10^8 [MPa \cdot s \cdot m^{-1}]$ (Coners, 2001). To convert the values of Coners (2001) we estimated the total root surface of an average pine tree of the *P1* stand with our simulated fine root biomass and the specific root area for Scots pine given in Ostonen et al. (2007). The value given by Williams et al. (2001a) was converted also with our simulated fine root biomass to refer the root resistance on the whole tree. Therefore, the values of Coners (2001) were divided by $1430 m^2$ simulated fine root surface per tree and the values of Williams et al. (2001a) were divided by $2.2 \cdot 10^4 g$ simulated fine root biomass. In addition the unit of water in (Williams et al., 2001a) had to be converted from $[mmol]$ to $[m^3]$ to

get [$MPa \cdot s \cdot m^{-3}$]. Due to the fact that the water flux in the equation 2.16 of (Campbell, 1991) is related on unit leaf surface the total root resistance values were divided by the total leaf area of an average pine tree of *P1*. Here we also used our simulated leaf biomass and converted it to leaf area with the specific leaf area for Scots pine given in Xiao et al. (2006). The three total root resistance R_r^{tot} values (used in chapter 4) were divided by 171 m^2 .

2.3 *STAR 2.0* Climate Scenarios

The statistical regional climate model *STAR 2.0* had been developed at PIK (Orlowsky et al., 2008). The scenarios follow a stepwise temperature trend of 0.5 K related on the average of whole Germany. For every climate scenario 100 realizations were calculated which show variation concerning the precipitation pattern. In comparison to the temperature increase of the SRES A2-Scenario in 2060 the 1.5 K-scenario is very close. In 2100 the prolonged 2.0 K-scenario correlates with this SRES-Scenario (Fig. 2.5). On this graph it can also be shown that the two degree limit is exceeded by the 1.5 K-scenario in 2036 and 3.0 K-scenario already in 2018. In this work mainly the 0 K, 1.0 K, 2.0 K and the 3.0 K-scenario have been applied.

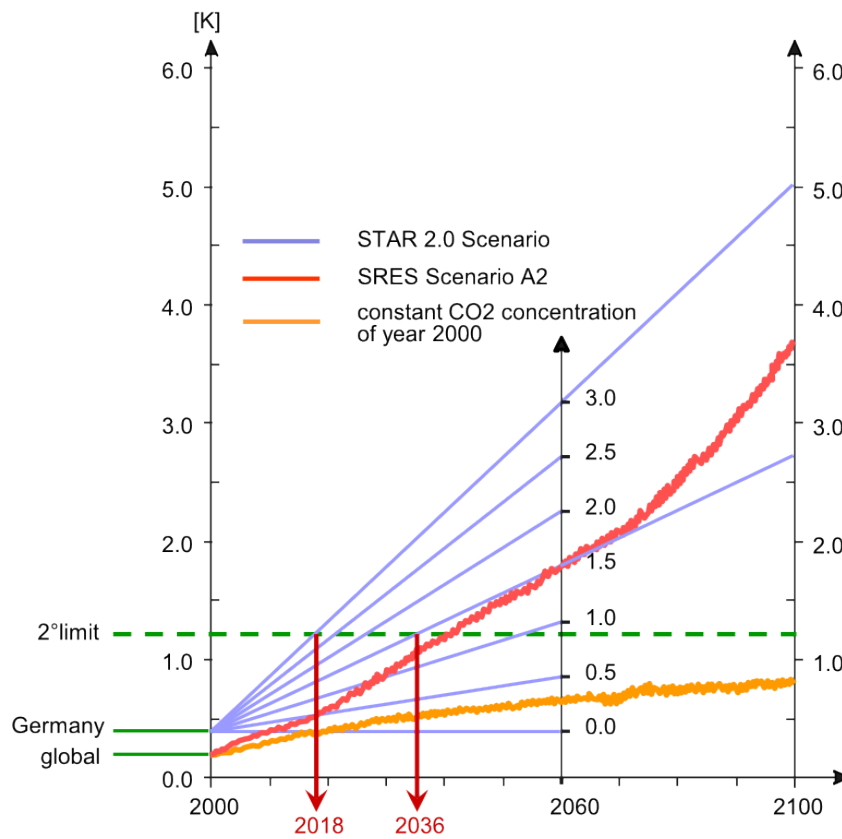


Figure 2.5: Overview of STAR 2.0 Scenarios with 0.5 K temperature increase step width (PIK, 2012)

Chapter 3

Evaluation of net primary production of four main tree species in Germany under climate change with static reduced models

3.1 Introduction

Climate change influences the components of ecological systems in different ways. Particularly with regard to the projected temperature rise for the next decades, a broad range of possible impacts on forest ecosystems is discussed (Alcamo et al., 2007). Furthermore forest ecosystems are key elements in the land-use matrix providing a variety of goods and services (Lindner et al., 2008; Maroschek et al., 2009). Thus, forests have to satisfy a variety of different and often conflicting needs in

social, ecological, and economic terms and under uncertain future conditions.

During the last 50 years the net primary production (NPP) of forests has increased in Europe (Ciais et al., 2008; Nemani et al., 2003; Spiecker, 2001). Besides changing management, age structure, forest area and nutrient balances also factors related to climate change partly explain this trend. Firstly, photosynthesis is not saturated at current carbon dioxide concentration (CO_2) and thus tree growth may benefit from increasing atmospheric CO_2 concentrations (Körner, 2006; Norby et al., 2005). However, interactions between the drivers of tree growth complicate the relationship between the CO_2 response of photosynthesis and growth (Körner, 2006; Körner et al., 2005; Norby et al., 2010). Secondly, changes in climatic trends influence regional temperature and water balances and most likely enhance the productivity of forest ecosystems at sites which are not nutrient limited (Boisvenue and Running, 2006; Ciais et al., 2008).

On the other hand, drought stress decreases productivity and increase the predisposition to biotic (insect calamities, fungi infections) and abiotic disturbances (forest fire, storm events). For example, Norway spruce (*Picea abies* L. Karst.) forests impaired by drought stress are highly predisposed to bark beetle attacks (Wermelinger, 2004).

Simulation studies indicate that the niches of forest tree species are highly sensitive to climatic changes and as a result species distribution and composition may be altered (Thuiller et al., 2005). This will broaden the silvicultural portfolio in mountainous and other temperature-limited forest ecosystems. Beside this positive effect at the leading edge also negative effects at the trailing edge of species distributions are reported: Scots pine (*Pinus sylvestris* L.) in its southernmost range may experience reduced growth and survival with modest warming (Reich and Oleksyn,

2008). Beech (*Fagus sylvatica* L.) forests show a decrease in basal area growth due to long-term drought in the Appenines (Piovesan et al., 2008).

Consequently, numerous simulation studies strive to answer how sensitive the global and regional forest productivity is to climate change in the next decades (Lasch et al., 2005, 2002a,b; Piao et al., 2009; Sitch et al., 2008). However, climate impact studies using process-based forest models require detailed information such as soil, stand, and meteorological data which are usually not available for a broad set of sites in a region. Otherwise, results from studies on a global scale are of limited value for regional predictions due to the coarse resolution of the models. Therefore, regional, spatially explicit studies of climate impact on forests call for models with low data requirement applicable for a large set of stands. Furthermore, to account for uncertainties associated with climate change projections, it is necessary to use a broad variety of climate change scenarios to derive probabilities of the expected impacts. In process-based models this comes at the cost of large amounts of computing time. These limitations can be circumvented by applying static reduced models (SRM). SRMs are developed by regression analyses from a large amount of data generated with a dynamic process-based forest model. The term static reduced model is used to separate it from time sensitive dynamic models and complex process based models with high parameter demand. We rely on simulated data, since only limited NPP measurement data from forest experimental sites with varying site conditions and forest species are available. There is especially a deficit in long-term time series of measurement of carbon fluxes.

Therefore, the first aim of this study is to derive SRMs for four tree species (European beech, Norway spruce, Scots pine, and oaks (*Quercus robur* L. and *Quercus petraea* Liebl.)) which allow calculating the annual average net primary produc-

tion (NPP). The derivation is based on annual NPP values simulated with the process-based model *4C* (Lasch et al., 2005). Independent variables of the SRMs for NPP-prediction are climate and soil variables over a spectrum of mono-species forest stands with different site conditions. Secondly, this study aims for an analysis of the impacts of a broad variety of climate scenarios with the SRMs for the four selected tree species at a large amount of sites all over Germany. Hence, we analyse two main questions: Which regional trends in NPP change are projected until 2060 in Germany? How much varies the SRM-based NPP calculation under a broad set of climate change scenarios and their realizations? This variety serves as an indication for the uncertainty of climate change scenarios.

3.2 Material and Methods

Climate data and climate scenarios

Observed and homogenised meteorological time series for the period 1951-2006 with daily resolution are available for 2342 meteorological stations at PIK (Österle et al., 2006). All stations are located in Germany, besides five in Switzerland and Austria. The meteorological data set provides information per station on climate parameters (e.g. total radiation, maximum temperature, mean temperature, minimum temperature, precipitation, total radiation).

Based on these observed daily meteorological data, climate change scenarios from 2007 until 2060 with daily resolution at the 2342 climate stations were derived with the statistical regional climate model STAR 2.0 (Orlowsky et al., 2008). In this study the observed meteorological data and 50 realizations of a climate change scenario based on the A1B SRES scenario (Nakicenovic et al., 2000) with a mean tempera-

ture increase in Germany of about 2 K until 2060 were used to simulate the NPP with *4C*. These simulations provide the data set for deriving the SRMs.

Furthermore, we used seven climate scenarios generated with STAR 2.0 assuming a 0.5 K stepwise increase of temperature up to 3 K. For example the 2 K climate scenario contains a temperature increase of 2 K in 2060 against the starting point of the scenario in 2007. For each of the seven climate scenarios (0 K, 0.5 K,..., 3 K) 50 realizations were available. All in all, the SRMs were then run with seven times 50 climate realizations.

Characteristics of the climate scenarios

At first, the change of four climate factors (mean annual temperature, mean annual precipitation sum, mean annual radiation, mean annual drought index) between the period 1951-2006 and 2031-2060 over all climate stations was analysed. The analysis of the seven applied climate scenarios described above indicated that besides the temperature increase, an increase of the radiation and the drought index shaped the climate scenarios for all climate stations. Only a slight trend to lower annual precipitation sums was calculated across the climate stations (Fig. 3.1 A-D).

3.3 Derivation of the static reduced model (SRM)

Model runs with *4C*

The average annual NPP data to be used for the regression analysis were calculated separately for mono-specific stands of the four tree species with *4C* at the 2342 climate stations in Germany. At each station four different soil types were assumed.

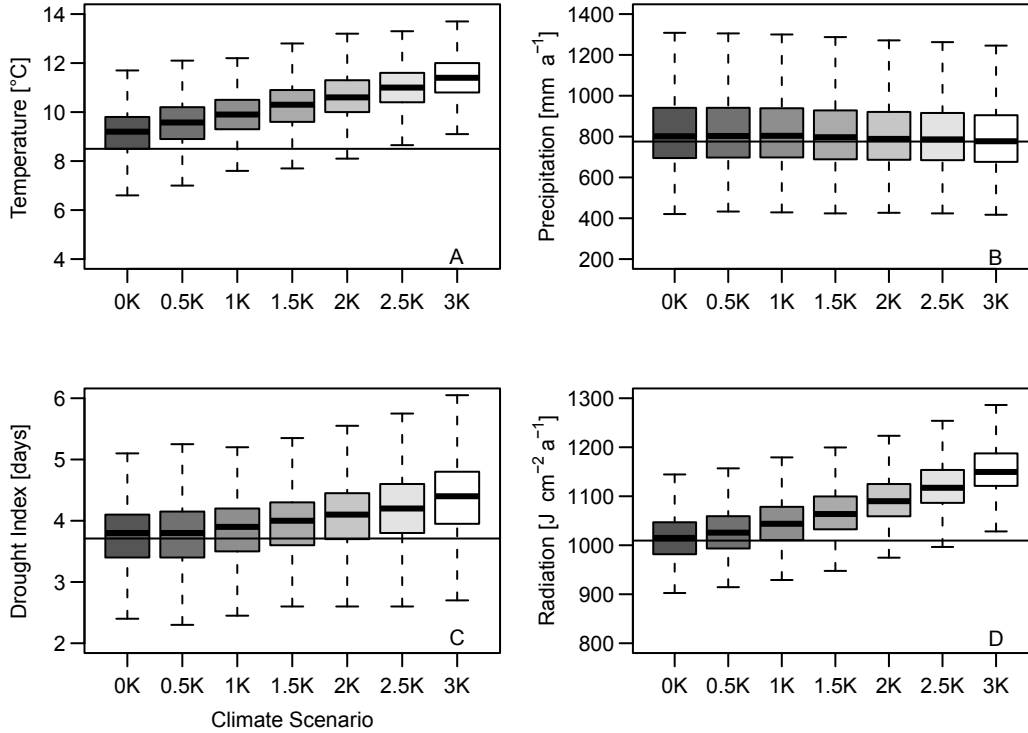


Figure 3.1: Change of climate factors depending on the climate scenario for all 2342 climate stations for 2031-2060 (A= X_T ; B= X_P ; C= X_D ; D= X_R). Black horizontal line represents average of 2342 climate stations for 1951-2006.

Hence, we simulated the average annual NPP for every tree species and soil type with the observed climate data of a climate station (1951-2006) and the future climate scenario based on the A1B emission trend (2007-2060). The soil types were parameterized for $4C$ on the base of four reference profiles of the soil database for Germany (BÜK 1 000, BGR 1998). They differ in the amount of plant available water and the carbon/nitrogen ratio (Tab. 3.1):

- poor soil with low water availability (PL)
- rich soil with low water availability (RL)

Table 3.1: Soil characteristics for the four selected soil types.

type	symbol	W_{PAW} [mm]	C_{tot} [g m ⁻²]	N_{tot} [g m ⁻²]	C_{tot}/N_{tot}
cambisol	PL	108	19650	640	31
cambisol	RL	69	4250	262	16
cambisol	PH	196	19650	640	31
cambisol	RH	156	4250	262	16

Table 3.2: Stand characteristics for the simulated mono-specific forest stands.

species	age [year]	d_{bh} [cm]	h_{dh} [m]	N_{stem} [ha ⁻¹]
oak	15	2.2	11.0	5734
pine	15	4.6	7.7	6664
spruce	15	3.3	6.0	7000
beech	15	2.7	6.5	6463

d_{bh} ... mean diameter at breast height of tree stand

h_{dh} ... dominant height of tree stand

N_{stem} ... number of trees

- poor soil with high water availability (PH)
- rich soil with high water availability (RH)

The stands were simulated for a time period of 56 years. The stand data for the initialization of $4C$ originate from yield tables (Tab. 3.2). We only considered young stands with an initial age of 15 to simulate the period with the highest annual productivity of an even-aged forest stand. The simulated annual NPP was averaged over the simulation period. To eliminate extreme sites, only sites with a simulated average annual NPP value $Y_{NPP_{4C}}$ greater than one ton carbon per hectare and year were considered for deriving the species-specific regression functions. That resulted in 2340 (climate stations) times four (soil types) times two (base and future climate

scenario), hence 18720, simulated average annual NPP values ($Y_{NPP_{4C}}$) for each of the tree species.

Fitting of the static reduced models

The functions for NPP were fitted to $Y_{NPP_{4C}}$ in dependence of climate and soil variables. We pre-selected soil and climate variables which could be important to accurately calculate the long-term average NPP simulated by $4C$. In the case of soil variables plant available water and the C/N ratio of the soil were chosen because they can be gathered easily from the German soil database. In the case of climate variables we started with variables available from climate stations (i.e. mean, minimum and maximum temperature, precipitation, radiation, air humidity, cloudiness and water vapour pressure) as well as aggregated climate variables such as climatic water balance and a drought index (see below) that could be derived from these measurements. To balance the amount of independent soil and climate variables and model accuracy, we decreased the amount of climate variables by forward selection. Hence, only variables with significant influence and a contribution to a better model fit (higher R^2) were added to the model. The analysis started with simple linear models without transformation of response and predictor values. The residuals of these linear models showed non-constant error variance and trends in the distribution, Hence, linear models with log-transformed response and predictor variables were tested. Also polynomial terms in the drought index variable were used to allow more flexible relationships leading to better fits. This resulted in multiple

regression functions with the same structure for all tree species:

$$\begin{aligned}
 \log(Y_{NPP_{SRM}}) &= \alpha + \beta_1(\log X_W) + \beta_2(\log X_{CN}) \\
 &+ \beta_3(\log X_T) + \beta_4(\log X_R) \\
 &+ \beta_5(\log X_D) + \beta_6(\log X_D^2) \\
 &+ \beta_7(\log X_W \log X_{CN}) + \varepsilon
 \end{aligned} \tag{3.1}$$

$Y_{NPP_{SRM}}$... annual average net primary production [$t\ C\ ha^{-1}year^{-1}$]

X_W ... plant available water [mm]

X_{CN} ... carbon/nitrogen ratio of the soil

X_T ... mean annual temperature [$^{\circ}C$]

X_R ... mean annual radiation [Jcm^{-2}]

X_D ... drought index [$days$], mean annual number of successive days without rain in the growing season

α ... intercept of regression

β_i ... regression coefficients

ε ... residual variance

The regression functions performance in comparison to the NPP values simulated with $4C$ ($Y_{NPP_{4C}}$) was assessed with the root mean squared error (RMSE), the relative root mean squared error (RMSE%), the absolute bias (BIAS), the relative bias (BIAS%) and the adjusted coefficient of determination (R^2) (Eq. 3.2-7). The distributions of the residuals were also examined. The derivation of the regression functions was conducted with the statistical software R (R Development Core Team,

2009).

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n}} \quad (3.2)$$

$$RMSE\% = \frac{RMSE}{\tilde{y}} \cdot 100 \quad (3.3)$$

$$BIAS = \frac{\sum_{i=1}^n (y_i - \hat{y}_i)}{n} \quad (3.4)$$

$$BIAS\% = \frac{BIAS}{\tilde{y}} \cdot 100 \quad (3.5)$$

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \tilde{y})^2} \quad (3.6)$$

$$R_{adj}^2 = 1 - \left[\frac{(1 - R^2)(n - 1)}{n - k - 1} \right] \quad (3.7)$$

y_i ... simulated with 4C $Y_{NPP_{4C}}$

\hat{y}_i ... simulated with SRM $Y_{NPP_{SRM}}$

\tilde{y} ... arithmetic mean of simulated $Y_{NPP_{4C}}$

n ... number of cases

k ... number of independent variables

3.4 Validation and plausibility of SRM results for NPP

To validate the SRMs for each tree species, we split the $Y_{NPP_{AC}}$ values into two equally-sized groups (model construction group, model validation group; (Vanclay and Skovsgaard, 1997)). The climate stations were sorted by latitude and every second station was reserved for the model validation group. Thus, both data sets cover entire Germany homogenously. The $Y_{NPP_{AC}}$ values and their corresponding independent variables of the model construction group were used to fit the regression function (Eq. 3.1). The resulting functions were then run with the independent variables of the model validation group to predict the $Y_{NPP_{SRM}}$ values and these were compared with simulated $Y_{NPP_{AC}}$ values of the validation group. Notice that the SRMs used for the climate change analysis were fitted to the full data set as described above (see section 2.3).

To check the plausibility of the SRMs, we compared the $Y_{NPP_{SRM}}$ values for the 1951-2006 period with two different observed data sets. The first data set by (Luyssaert et al., 2007) includes estimates of NPP for temperate forests in Central Europe. This data set was generated from peer-reviewed literature and CO₂ flux measurements. The second data set was taken from (Pretzsch, 2009) and is based on German forest inventory data. These two data sets provide independent estimates of the annual NPP of the four forest species used in this study.

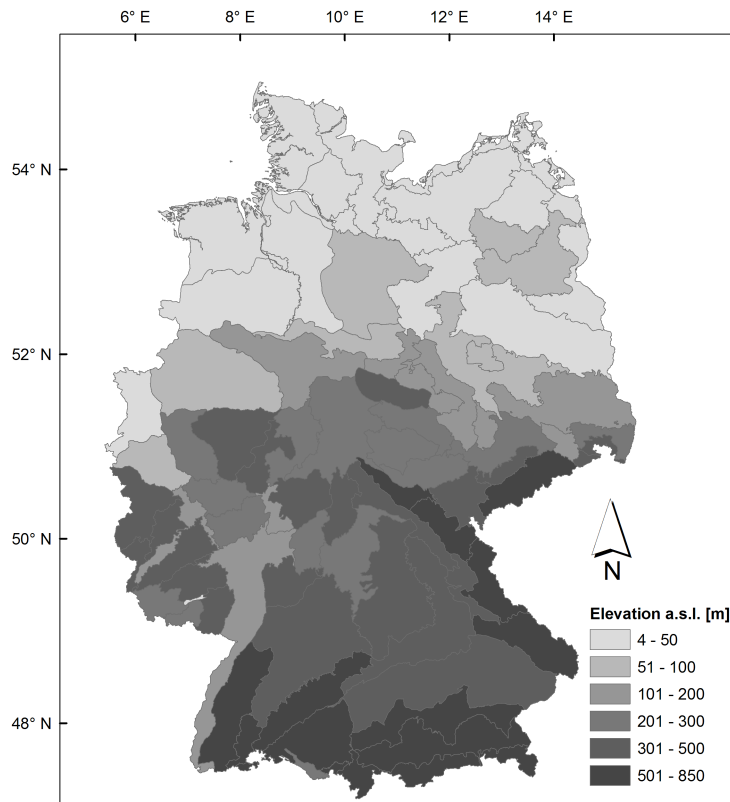


Figure 3.2: Forest eco-regions in Germany (after Wolff 2002) with the mean elevation derived from elevation of the climate stations.

3.5 Experiments and analyses with the SRMs

The SRMs were run with the seven climate scenarios covering a temperature increase from 0 K to 3 K until 2060. For each climate scenario consisting of 50 realizations, the average annual NPP of the four tree species, every climate station and the four different soil types was calculated with the SRMs. The variables required to drive the SRMs (see Eq. 3.1) were averaged for a 30 year time period from 2031-2060.

For the spatial comparison of NPP, the results have been aggregated by calculating the mean average annual NPP of the climate stations belonging to the same forest

eco-region (Fig 3.2). The forest eco-regions represent a classification of the area of Germany that includes forest site characteristics like climate, soil properties and geomorphologic aspects (Wolff, 2002). For further analyses we also calculated the mean elevation for each forest eco-region on the base of the station altitude (Fig. 3.2).

To test the sensitivity of the SRMs to each climate factor (temperature, radiation, drought index) we varying each factor from 40% to 200% around the total average value over all 2342 climate stations. This range covered well the expected range of factors encountered in the studied area. Only one factor was altered while the other factors were kept constant at their average value of all 2342 climate stations.

The range between the maximum and minimum NPP of the climate stations belonging to a forest eco-region under all 50 realizations indicates the uncertainty within a climate scenario. The larger the range, the higher is the variability of the climate realizations of a climate scenario.

3.6 Results

Model evaluation

The parameters of the four species-specific SRMs and their standard errors were derived from the regression analysis (Tab. 3.3). All parameters are highly significant from zero and in the same order of magnitude for the different species.

The analysis of the SRMs performance shows that they are suitable for estimating the average annual NPP as simulated with *4C* (Tab. 3.4). The values of NPP calculated by the SRMs are nearly unbiased with a relative BIAS smaller than one

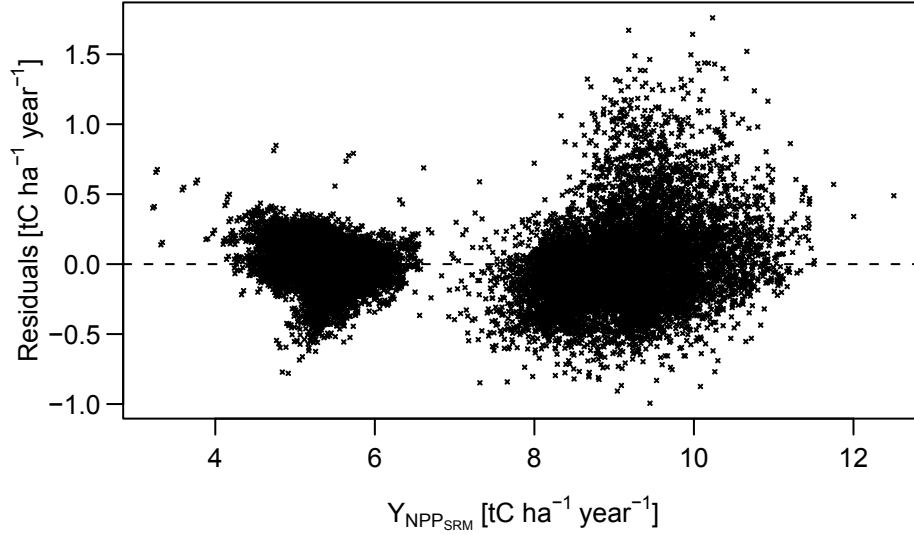


Figure 3.3: Distribution of the residuals of the SRM against fitted SRM values for Scots pine.

Table 3.3: Regression coefficients for the species-specific SRMs and their standard error (s.e.). Asterisk indicates significance at $p < 0.01$ level.

	beech		oak		pine		spruce	
	estimate	s.e.	estimate	s.e.	estimate	s.e.	estimate	s.e.
α	-4.016*	0.073	-4.753*	0.068	-4.534*	0.047	-4.273*	0.053
β_1	0.198*	0.010	0.181*	0.009	0.221*	0.006	0.265*	0.007
β_2	-0.753*	0.016	-0.853*	0.015	-0.540*	0.010	-0.622*	0.012
β_3	0.314*	0.003	0.465*	0.003	0.290*	0.002	0.252*	0.002
β_4	0.905*	0.007	1.015*	0.006	0.961*	0.004	0.928*	0.005
β_5	1.432*	0.031	1.293*	0.029	1.069*	0.020	1.011*	0.023
β_6	-0.543*	0.011	-0.486*	0.010	-0.413*	0.007	-0.394*	0.008
β_7	-0.056*	0.003	-0.052*	0.003	-0.061*	0.002	-0.076*	0.002

percent. The high R^2 indicates that the SRMs work equally well for all considered tree species. The SRMs differ only slightly in their statistical characteristics for the four tree species. Therefore, the next results are only shown for Scots pine if not

Table 3.4: Absolute and relative RMSE and BIAS and coefficient of determination of the average annual NPP ($t\ C\ ha^{-1}year^{-1}$) calculations with the SRMs compared to $4C$ at the stand level.

	beech	oak	pine	spruce
RMSE	0.290	0.256	0.248	0.203
RMSE%	5.054	4.662	3.433	3.964
BIAS	0.005	0.001	0.002	0.003
BIAS%	0.080	0.016	0.033	0.050
R^2_{adj}	0.978	0.984	0.987	0.988
n	18720	18720	18720	18720

indicated otherwise. There is no observed trend in the distribution of the residuals thus variance homogeneity can be assumed (Fig 3.3). The two data clouds result from the rich and poor soils (see Tab. 3.1).

The validation results from the partitioned datasets also prove the suitability of the SRMs. The coefficient of determinations for the linear regression between NPP calculated with the SRM ($Y_{NPP_{SRM}}$) for the model validation group and the corresponding values of NPP from $4C$ ($Y_{NPP_{4C}}$) (Fig. 3.4) is very high for all tree species (Tab. 3.5). However, for all tree species the intercept is different from zero and the slope differs from 1 (Tab. 3.5). Nevertheless, the discrepancy between the $Y_{NPP_{SRM}}$ and $Y_{NPP_{4C}}$ values is small.

The sensitivity analysis shows that the polynomial terms in the SRM describe the nonlinear relationship between the NPP and the drought index very well (Fig. 3.5 C). Similarly, the assumed log-linear relationship between NPP and temperature is obvious in the simulated $4C$ results, whereas the dependence between radiation and NPP was almost linear in the $4C$ results (Fig. 3.5A,B).

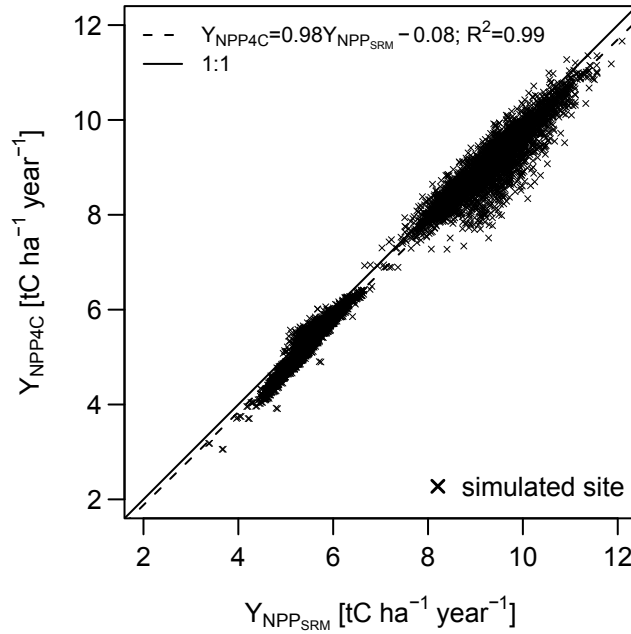


Figure 3.4: Scatter plot with $Y_{NPP_{SRM}}$ of the model validation group and $Y_{NPP_{4C}}$ and the regression line between both NPP values for the validation of Scots Pine.

Table 3.5: Results of the linear regression between $Y_{NPP_{SRM}}$ and the corresponding results of NPP from $4C$ $Y_{NPP_{4C}}$ for the validation.

	Equation $Y_{NPP_{4C}} =$	R^2
beech	$0.98Y_{NPP,SRM} - 0.2$	0.98
oak	$1.03Y_{NPP,SRM} - 0.3$	0.99
pine	$0.98Y_{NPP,SRM} - 0.08$	0.99
spruce	$0.96Y_{NPP,SRM} - 0.01$	0.99

Comparison of SRM results with observed data

The mean annual NPP values calculated with the SRMs for the four tree species vary from $3.5 \text{ t C ha}^{-1}\text{year}^{-1}$ for to $9.1 \text{ t C ha}^{-1}\text{year}^{-1}$ (Fig 3.6). For Scots pine on poor soils (PL and PH, see Tab. 3.1) there is a good correspondence between the

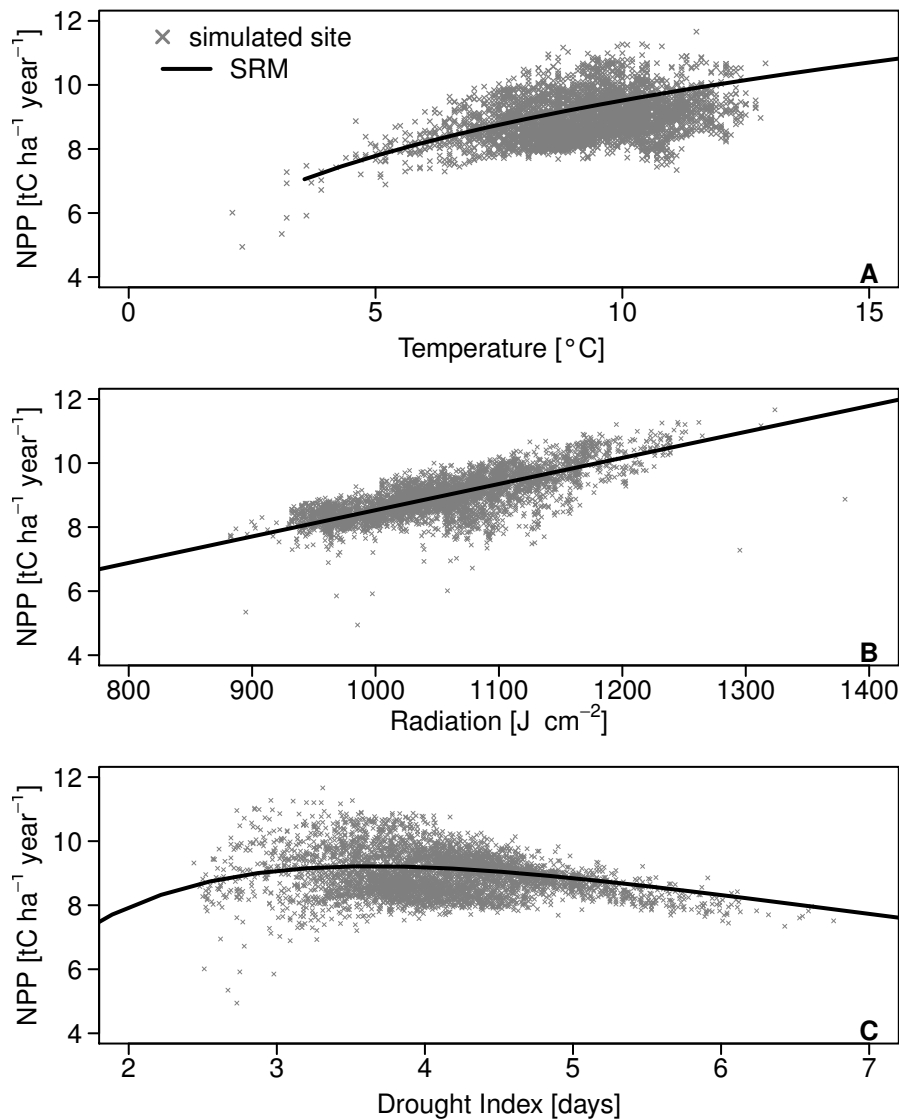


Figure 3.5: Simulated NPP with $4C$ (grey crosses) for Scots pine on rich soils with low water availability and sensitivity of the SRM (black line) to changes in the parameter value for temperature (A), radiation (B) and the drought index (C) while the other climate factors ($X_T=8.9^\circ\text{C}$, $X_R=1082\text{ J cm}^{-2}$, $X_D=3.9\text{ days}$) are fixed.

SRM and the values of (Luyssaert et al., 2007) and (Pretzsch, 2009). For Scots pine on rich soils (RL and RH, see Tab. 3.1) the NPP values of the SRM are highest

compared with the other tree species. For Norway spruce, oak and beech a good correspondence between SRM values and observed data can be stated in case of rich soil conditions. In contrast, the NPP values of the SRMs for beech, oak and Norway spruce on poor soil conditions are lower in comparison with the two data sets (Fig 3.6).

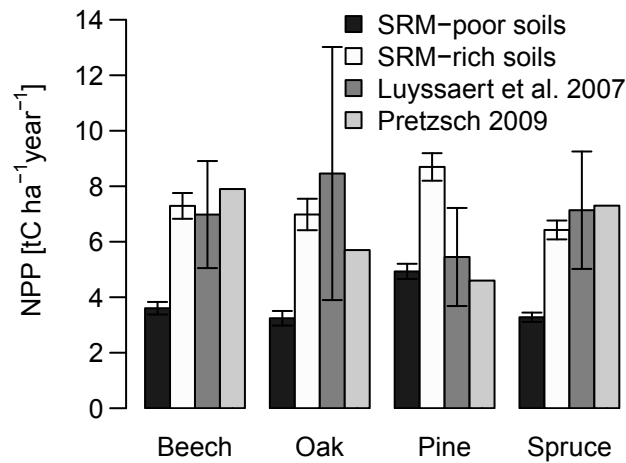


Figure 3.6: Comparison of the NPP estimated with the SRMs on poor and rich soils (averaged over high and low plant available water) and two observed data sets for the four tree species. Error bars indicate one standard deviation.

Overall characteristics of the net primary production calculated with the SRMs

The tree species with the highest NPP calculated by the SRMs over the 2342 climate stations is Scots pine. The NPP of all four tree species on rich soils is around twice the NPP of the poor soils (Tab. 3.6). There is almost no difference in terms of NPP between the soils with low and high plant available water (Tab. 3.6). The sensitiv-

ity of NPP to climate factors is most pronounced on rich soils. The range between the minimum and the maximum NPP of a forest stand at a specific climate station is smaller on poor soils. There is an overall trend to rising NPP with increasing temperature trend for the analysed stands. However, there are differences between the tree species.

Table 3.6: Minimum, maximum and median of simulated average annual NPP over all forest eco-regions with the total range of simulated NPP

site	species	value	0K	0.5K	1.0K	1.5K	2.0K	2.5K	3.0K
PL	beech	min	2.1	2.2	2.3	2.5	2.6	2.8	3.0
PL	beech	median	3.8	3.8	4.0	4.1	4.2	4.3	4.5
PL	beech	max	4.8	4.9	5.0	5.2	5.4	5.5	5.6
PL	oak	min	1.6	1.7	1.8	2.0	2.2	2.4	2.6
PL	oak	median	3.4	3.5	3.7	3.8	4.0	4.1	4.3
PL	oak	max	4.6	4.7	4.9	5.1	5.3	5.4	5.6
PL	pine	min	3.1	3.2	3.4	3.6	3.8	4.1	4.4
PL	pine	median	5.1	5.2	5.4	5.5	5.7	5.9	6.1
PL	pine	max	6.6	6.8	7.0	7.2	7.4	7.5	7.8
PL	spruce	min	2.2	2.3	2.4	2.5	2.6	2.8	3.0
PL	spruce	median	3.4	3.5	3.6	3.6	3.8	3.9	4.0
PL	spruce	max	4.4	4.5	4.6	4.7	4.8	4.9	5.1
PH	beech	min	2.1	2.2	2.3	2.5	2.6	2.8	3.0
PH	beech	median	3.8	3.9	4.0	4.1	4.2	4.3	4.5
PH	beech	max	4.8	4.9	5.1	5.2	5.4	5.5	5.7
PH	oak	min	1.6	1.7	1.8	2.0	2.2	2.4	2.6

site	species	value	0K	0.5K	1.0K	1.5K	2.0K	2.5K	3.0K
PH	oak	median	3.5	3.6	3.7	3.8	4.0	4.1	4.3
PH	oak	max	4.6	4.8	4.9	5.1	5.3	5.4	5.6
PH	pine	min	3.1	3.2	3.4	3.6	3.8	4.1	4.4
PH	pine	median	5.1	5.3	5.4	5.5	5.7	5.9	6.1
PH	pine	max	6.7	6.8	7.0	7.2	7.4	7.6	7.8
PH	spruce	min	2.2	2.3	2.4	2.5	2.6	2.8	3.0
PH	spruce	median	3.4	3.5	3.6	3.7	3.8	3.9	4.0
PH	spruce	max	4.4	4.5	4.6	4.7	4.8	4.9	5.1
RL	beech	min	4.0	4.2	4.4	4.7	5.0	5.4	5.8
RL	beech	median	7.2	7.4	7.6	7.8	8.0	8.3	8.5
RL	beech	max	9.2	9.4	9.7	10.0	10.3	10.5	10.8
RL	oak	min	3.3	3.5	3.7	4.1	4.4	4.8	5.2
RL	oak	median	7.0	7.2	7.5	7.7	8.0	8.3	8.7
RL	oak	max	9.3	9.6	10.0	10.3	10.7	11.0	11.4
RL	pine	min	5.2	5.5	5.7	6.1	6.5	6.9	7.4
RL	pine	median	8.6	8.8	9.1	9.3	9.6	9.9	10.3
RL	pine	max	11.2	11.5	11.8	12.1	12.5	12.7	13.1
RL	spruce	min	4.1	4.2	4.4	4.7	4.9	5.2	5.6
RL	spruce	median	6.3	6.5	6.6	6.8	7.0	7.2	7.4
RL	spruce	max	8.2	8.3	8.5	8.8	9.0	9.1	9.4
RH	beech	min	4.2	4.3	4.6	4.9	5.2	5.6	6.0
RH	beech	median	7.5	7.6	7.9	8.1	8.3	8.6	8.9
RH	beech	max	9.5	9.8	10.0	10.3	10.7	10.9	11.2
RH	oak	min	3.4	3.6	3.9	4.2	4.5	4.9	5.4

site	species	value	0K	0.5K	1.0K	1.5K	2.0K	2.5K	3.0K
RH	oak	median	7.2	7.4	7.7	8.0	8.3	8.6	9.0
RH	oak	max	9.6	9.9	10.3	10.6	11.1	11.3	11.8
RH	pine	min	5.4	5.7	6.0	6.4	6.7	7.2	7.7
RH	pine	median	9.0	9.2	9.4	9.7	10.0	10.3	10.7
RH	pine	max	11.7	11.9	12.3	12.6	13.0	13.2	13.7
RH	spruce	min	4.2	4.4	4.6	4.9	5.1	5.5	5.8
RH	spruce	median	6.6	6.8	6.9	7.1	7.3	7.5	7.8
RH	spruce	max	8.5	8.7	8.9	9.1	9.4	9.5	9.9

The median of the range within a climate scenario alternate around $0.5 \text{ t C ha}^{-1}\text{year}^{-1}$ for all tree species. There is a slight trend to rising median of ranges with the temperature increase of the climate scenarios. Also, the the 1.5-fold interquartile distance of the ranges increases with temperature increase, except for Norway spruce (Fig. 3.7).

Regional specific analyses of the impact model for pine

Because the spatial pattern and trends in NPP are similar for the tree species, in the following only results for Scots pine are shown. The positive effects of climate change are stronger in mountainous regions where temperature is an important limitation of NPP (Fig. 3.8). In general, the Scot pine sites with the lowest increase in NPP are located in low lands. The lowest NPP increase for Scots pine, as the median of 50 realizations with the 3 K scenario, varies from 114 % to 116 % (Fig.

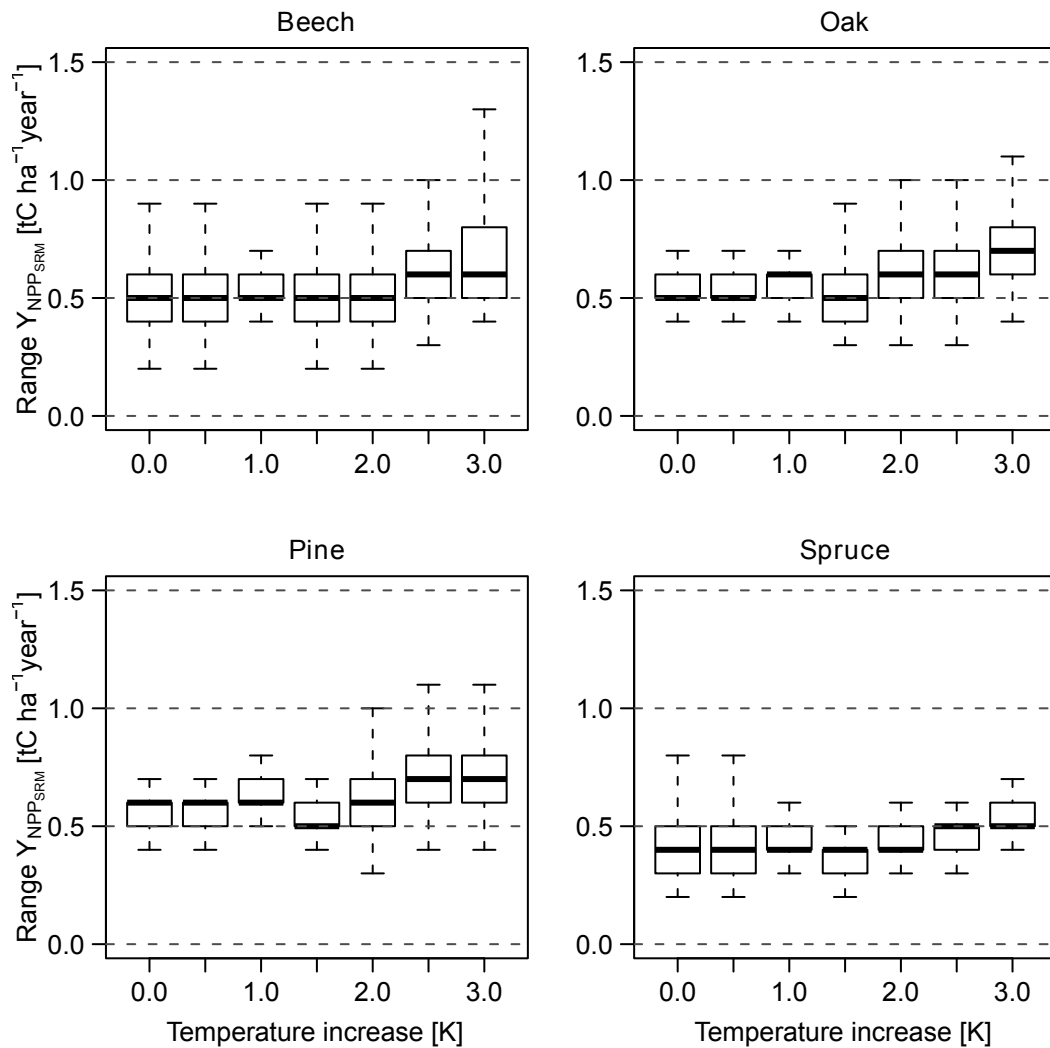


Figure 3.7: Boxplot with estimated $Y_{NPP_{SRM}}$ range of the 50 realizations of every climate scenario for 2342 climate stations for four tree species and RL site conditions. Boxes show the lower quartile (25%), the median (50%) and the upper quartile (75%). The whiskers represent the 1.5 fold interquartile range.

3.8).

To measure the uncertainty of climate change predictions, the range of $Y_{NPP_{SRM}}$ was calculated according to the 50 realizations for each eco-region. The maximum

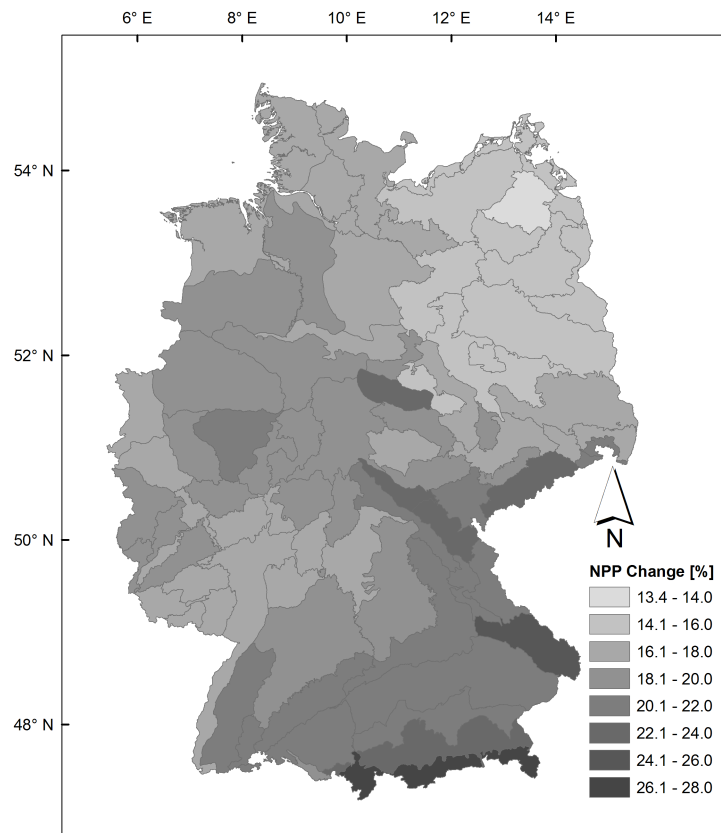


Figure 3.8: Map of the interpolated relative increase in calculated NPP of Scots pine on rich soils with low water availability for 2031-2060 as median of the realisations for the 3 K scenario compared with the calculated NPP for the 0 K Scenario. Black lines are the boundary lines for the forest eco-regions.

range for the realizations of the 3 K climate scenario is $1.6 \text{ t C ha}^{-1}\text{year}^{-1}$ in the north-eastern forest eco-regions of Germany. In the southern, western and mountainous eco-regions different realizations lead to a range of only $0.8 \text{ t C ha}^{-1}\text{year}^{-1}$ with the minimum occurring in mountainous regions (Fig. 3.9).

There is a clear trend in the pattern of impacts on NPP for the forest eco-regions. The forest eco-regions with higher elevation benefit more from the projected climate change while forest eco-regions in the lowlands show higher uncertainty within the

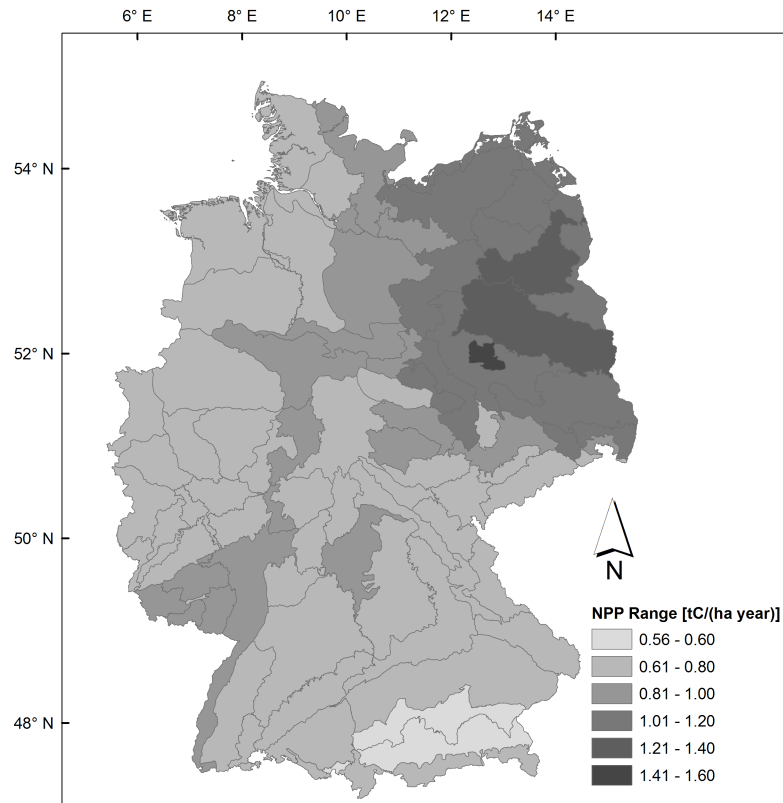


Figure 3.9: Map of the average range of NPP of Scots pine on rich soils with low water availability for the eco-regions under the 3 K scenario. Black lines are the boundary lines for the forest eco-regions.

realizations of a climate scenario (Fig. 3.10).

3.7 Discussion

This study focuses on the development of SRMs for evaluating the impact of climate change on forest productivity on regional scale. In a first step, regression functions with soil and climate factors as independent variables and the average annual NPP

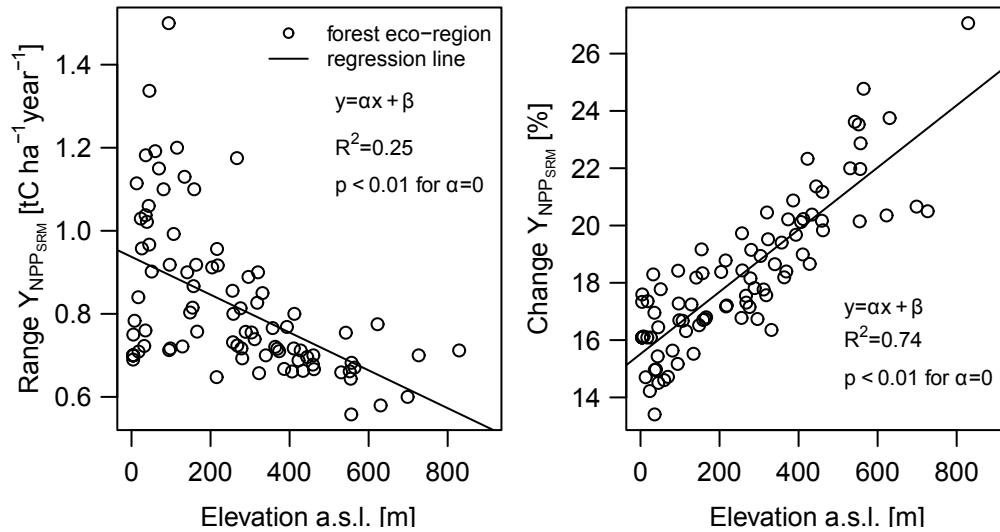


Figure 3.10: Relationship between the mean elevation of a forest eco-region and the NPP range (left) and NPP change (right) of Scots pine. The NPP change is the difference between the NPP values of the 0 K climate scenario and the 3 K climate scenario for the 2031-2060 period. The range is the difference between the maximum and the minimum NPP within the 50 realizations.

as dependent variable were derived from the average annual NPP values simulated with the process-based forest growth model *4C* for a broad set of stands and site conditions. Fitting these functions for the four tree species resulted in SRMs. The SRMs allow calculating the average annual NPP of a forest stand with less site parameters and climate data than required by a process-based model like *4C*. These SRMs were applied on different climate change scenarios to analyse the effects on forest eco-regions in Germany.

Model evaluation and validation

The goodness of fit between simulated NPP with $4C$ and simulated NPP with the SRMs is very high in the case of all considered tree species. The model bias and root mean square error are low and there are only few sites with deviations larger than $1 \text{ t C ha}^{-1}\text{year}^{-1}$. The soil plant available water and the carbon/nitrogen ratio were selected as independent variables describing the site conditions. They can be derived easily from basic soil information such as the BUEK 1000 (BGR, 1998), or similar databases as from the European Soil Data Centre (ESDAC). Process-based models such as $4C$ require a more detailed site description with physical and chemical soil properties which are not commonly available for a broad set of sites. Temperature, radiation and a drought index were chosen as climate independent variables for the SRM. This approach also represents a reduction of input data requirements as compared to process-based models which typically also include precipitation, relative humidity, air pressure, wind velocity (Fontes et al., 2010). The selected climate and soil variables determine most of the variance in the average annual NPP simulated by $4C$. The sensitivity analysis of the climate variables shows a good agreement in the logarithmic relationship between temperature and $Y_{NPP_{4C}}$. In case of the drought index the polynomial term allows the best fit. In spite of the linear relation between radiation and $Y_{NPP_{4C}}$ we keep the log-transformation of radiation to have all independent variables at the same logarithmic scale.

Also the model validation by partitioning the dataset for model fitting into a model construction and a model validation dataset did not reveal serious model errors (Tab. 3.5). However, the partitioning of the dataset does not produce a totally independent data set. Thus the validation does not supply further information about model biases which is also reported for other cross-validation methods (Vanclay and

Skovsgaard, 1997; Kozak and Kozak, 2003).

Henceforth, the SRMs could be run with a large set of climate scenarios to assess regional climate impacts on forest productivity. The resulting NPP represents a potential NPP depending on the assumed soil characteristics and the climate. Moreover, the NPP simulated with $4C$ that have been used to derive the SRMs, represent only young, productive stands (age 15-70). Therefore, the NPP values calculated with the SRMs are higher compared to middle-aged and old forest stands. The SRMs average mean annual NPP of 3 to 10 t C $ha^{-1}year^{-1}$ is in accordance with a simulation study by (Oene et al., 2000). They calculated the NPP over a broad spectrum of Norway spruce and beech forest stands in Europe ranging from 3 to 12 t C $ha^{-1}year^{-1}$. (Jochheim et al., 2009) simulated NPP values between 5 and 7 t C $ha^{-1}year^{-1}$ for Scots pine, beech and Norway spruce forests on nine level II. plots in Germany. Similarly to the results of this study, they revealed that the differences in NPP between sites are larger than between the tree species.

In comparison with the data sets of (Luyssaert et al., 2007) and (Pretzsch, 2009), our NPP values of Scots pine seem too high (Fig. 3.6). However, Scots pine stands are very often situated on less productive sites in Germany. Therefore the SRM values of the poor sites represent the actual species distribution more realistically and really fit much better to the observed data. In case of beech and oak, the SRM values on rich sites are in the range of the two data sets, which yet again reflects the distribution of these species on forest soils in reality. The general lower NPP values of Norway spruce calculated with the SRMs cannot be explained by site-specific characteristics. Here, a systematic bias in the simulated NPP with $4C$ could be present and needs to be further investigated.

The C/N ratio as a measure for nitrogen availability reflects the relationship be-

tween nitrogen availability and NPP and was also found by (Oene et al., 2000). The model *4C* could simulate reduced tree productivity at poor soils mainly due to nitrogen limitation. Simultaneously, the NPP is low and therefore, other factors like the water supply have a small influence on the average annual NPP. If nitrogen limitation is not simulated on rich soils, climate factors like temperature and precipitation have higher impact on simulated NPP which explains the greater range in NPP on these soils. In spite of its weak influence in this study, plant available water is usually an important site factor for tree productivity under climate change (Kellomaki and Wang, 2000). One reason for our finding could be a low level of simulated drought stress by low soil water contents with *4C*. On the other hand, a strong negative correlation between the drought index greater than four and NPP for water limited sites could be stated according to the SRMs (estimated threshold from Fig. 3.5). Small changes in precipitation sum or in drought index lead to stronger responses of the SRMs in these water-limited regions such as described in other studies (Gerten et al., 2008; Sang and Su, 2009). The positive relationship between mean annual temperature and NPP in the SRMs is in good accordance with investigations in temperate forests (Boisvenue and Running, 2006; Oene et al., 2000; Piao et al., 2009).

Climate impact analysis

For Germany, the average annual NPP calculated with the SRMs increases until 2060 for all climate scenarios and all tree species. This result supports the findings of other studies that the terrestrial carbon sinks should peak around 2050 (Piao et al., 2009; Sitch et al., 2008). In Germany two main regions could be identified

where climate change impacts on NPP are most pronounced. Firstly, in mountainous region the temperature increase will strongly enhance the NPP. A maximum value of 28 % increase of NPP for Scots pine forest stands has been calculated by the SRM for the 3 K scenario (Fig. 3.8 and Fig. 3.10). In comparison, (Oene et al., 2000) simulated an increase of NPP at maximum 11 % only considering the direct effects of a temperature increase of 2 K. Different precipitation pattern of the scenario realizations affects the NPP in regions with high precipitation only slightly. Secondly, in the north-eastern lowlands of Germany the potential temperature-induced increase of NPP is limited by the drought duration during the growing period. Here the change of NPP of the 3 K scenario is about 13-16 % and is accompanied by a higher uncertainty range of the scenario (Fig. 3.8 and Fig. 3.9). The outcomes of temperature increase are site-specific considering also the effect of temperature increase on plant water relations: a rising transpiration demand results in more frequent stomata closure on water-limited sites which reduces the NPP. Thus, there is a high relevance of future precipitation patterns in the realizations according to calculated NPP in regions with low annual precipitation sums today.

Applicability of the SRMs

Our analyses highlight the advantage of the SRMs as a tool for efficient analyses of broad sets of climate scenario realisations for a large amount of sites. A simulation experiment with a set of 2342 sites times four soil types and four tree species with 50 realizations of 7 climate scenarios for a simulation period of 30 years with the model *4C* would require 150 days of CPU time whereas running the SRMs takes 30 minutes. Furthermore, as shown above, there is less demand of input data for

model application, compared to a process-based model like *4C*. The SRMs need only two site characteristics, which can be derived from soil data bases, and long-term mean values of climate data. Their application supports detecting regions that face high climate impacts and allows subsequent efficient investigation of vulnerable forest stands with more complex process-based models or cost-effective measurements methods. Thus, the SRMs do not substitute analyses with process-based models but rather complement them.

Another way to derive SRMs for NPP could be by using measurement data for carbon fluxes instead of model simulation data. However, thus far the low variation of site conditions and species at the flux sites in Germany, the comparably short time periods covered and difficult data availability hamper this approach. The use of other data sources of forest productivity like the National Forest Inventory in Germany could be a valuable data source but therefore repeated measurements are required which are not available for all federal states in a standardized format.

On the other side, there are also disadvantages of the SRMs. These models do not allow the analysis of annual or seasonal cycles of NPP or of productivity in mixed stands. Also questions related to reduced productivity due to biotic disturbances or extreme events in forest stands cannot be answered and should be further investigated.

3.8 Conclusion

Static reduced models (SRM) can be used as simple impact functions to determine regional impacts on the productivity of mono-specific forest stands under climate

change scenarios. The SRMs permit a spatial overview on general trends of productivity change under climate change and thus help to identify regions which are likely to be most vulnerable.

Running the SRMs with a broad range of temperature increases and different precipitation levels reveal a generally positive impact on the productivity of the four main tree species in Germany. The NPP increases for all tree species with rising temperatures especially on temperature-limited sites such as mountainous regions or on sites with high precipitation. However, beyond a 2 K temperature increase until 2060, the uncertainty of NPP on water-limited forest sites is also increasing. Here, the results indicate a high risk of decreasing NPP for Norway spruce, Scots pine and beech. The NPP of oak on these sites is less sensitive. These rapid analyses can inform and thus complement more detailed analysis with process-based models. Especially on sites with high impacts of precipitation patterns on the productivity of forest stands we recommend to further analyze climate impacts with process-based forest growth model or detailed measurements.

Further research should focus on an improved validation of the SRMs with regard to soil factors and forest productivity.

Chapter 4

Modeling of two different water uptake approaches for mono- and mixed-species forest stands with *4C* - Model validation across scales

4.1 Introduction

The alteration in environmental conditions due to climate change influences the components of ecological systems. Particularly the predicted temperature rise for the next decades entails a large variation of possible impacts on forest ecosystems (Alcamo et al., 2007). Various model studies have examined the response of forest

growth to changing climate conditions to develop future forest management strategies ensuring ecologically viable forest ecosystems (Lasch et al., 2005; Lindner and Cramer, 2002; Pussinen et al., 2009).

Resistance to drought stress is an important factor for the functioning of many forest ecosystems, because of the close relationship between carbon and water cycles in trees expressed by the linkage of stomatal conductance and photosynthesis (Farquhar and Sharkey, 1982; Jarvis and Davies, 1998). Climate warming includes the effect of decreasing water availability due to higher evapotranspiration rates in most European regions. In Mediterranean forests, the morphology, phenology and physiology of trees is well-adapted to recurring drought events (Scarascia-Mugnozza et al., 2000). In Central Europe, severe droughts are less frequent and thus the adaptation to drought stress is less distinctive. Especially, the growth of mature forest stands is strongly dependent on water availability during the growing period (Breda et al., 2006).

In the federal state of Brandenburg, Germany 70% of forest area is stocked with pure Scots pine (*Pinus sylvestris* L.) stands which are partly being converted to mixed Scots pine-oak stands (*Quercus petraea* [Matt.] Liebl.). The region combines dry climate conditions and soils with low water storage capacity. The vulnerability of Scots pine to severe drought events has been discussed for several years (Galiano et al., 2010; Poyatos et al., 2007). In addition, the stability of pure Scots pine stands is unclear at the southern and western areal borders of the habitat under the condition of continuous temperature increase in the next decades (Rebetez and Dobbertin, 2004).

Therefore, assessing the magnitude of severe drought impacts in the future is essential. Doing so requires the realistic mapping of plant available water which represents

the water supply to tree roots. There are two theories on water flow within trees. First, the cohesion-tension theory of the ascent of sap deals with the physics of the sap water movement. Second, the electrical analogy describes the water transport within the soil-plant-water continuum by using resistances, capacitances, and water potentials (Cruiziat et al., 2002).

Process-based forest growth models are scientific tools suitable to study climate impacts and tree responses to droughts (Holst et al., 2010; Keenan et al., 2009, 2010; Wang et al., 2008). Forest canopy models for the soil-plant-atmosphere-continuum as developed by (Williams et al., 1996) link carbon uptake of forest stands to weather conditions and soil properties. They can provide reliable information about the relationships between carbon dioxide uptake, stomatal conductance and transpiration. The water flow is described as an electrical circuit and water uptake of roots is simulated by calculating water flow dependent on the water potential gradient from soil to atmosphere (Campbell, 1991; Doussan et al., 1998; Grant et al., 2005; Hacke et al., 2000; Williams et al., 2001a,b). The considered water potentials and resistances depend nonlinearly on the water contents in the particular components along the soil-plant-atmosphere-continuum (SPAC). The maximum rate of water supply by roots is determined by the minimum sustainable leaf water potential, the soil conductivity for water flow and the root resistance to water uptake. This approach permits a species-specific characterization of belowground competition in mixed forest stands since modeling of resistances of root water uptake directly depends on relative fine root length densities, a species-specific, measureable parameter. The SPAC-model predicts varying stomatal conductance so that daily carbon uptake is maximized within the limitations of canopy water and nitrogen availability. However, the described model by (Williams et al., 1996) is less useful to analyze impacts

of extreme weather events (e.g. droughts) on diameter increment and subsequently timber yield of forest stands. For this purpose, models are required that incorporate a carbon allocation module and consider stand development with regard to management and mortality. Economic and ecological sustainability under continuous climate warming can be investigated with these kinds of forest growth models. However, in these models usually a simple function accounts for limited water uptake at decreasing soil water content. They simulate water uptake with an empirical reduction function which is linearly dependent on soil water content (Grote and Suckow, 1998; Kirschbaum, 1999).

Due to the complexity of comparing these two approaches with regard to direct and indirect effects on different model output variables (e.g. soil water limitation reduction of transpiration reduction of diameter increment) three different data sets are employed to discuss the results at several tree growth relevant time scales. Hence, the data sets include 1) daily transpiration and 2) soil water content measurements over a short-term period which provide a direct link to root water uptake. In addition 3) annual tree ring data serve as a long term validation archive for severe drought events which constitute an indirect link to root water uptake impacts (Beniston, 2010).

Knowledge about the sensitivity of different water uptake model approaches within a physiological-based forest growth model helps to detect and discuss potential severe drought events under future climate scenarios. Furthermore, it is of major importance for the development of suitable tools for planning adaption strategies. The objective of this paper is to identify the effect of two commonly used water uptake approaches on the simulated amount of plant available water and to assess the resulting effects on tree growth. Both approaches are implemented in the pro-

cess based forest growth model $4C$ (FORESEE - FORESt Ecosystems in a changing Environment) (Lasch et al., 2005) and applied in a simulation study. This simulation study strives to respond to the following questions: 1) Are there differences between both approaches regarding the water supply by the roots? 2) Is there an approach which performs best regarding all three validation data sets? 3) How well can drought years, observed by annual tree ring analyses, be reproduced by the different water uptake approaches?

4.2 Material and Methods

Modelling water uptake

The water uptake approach (WU1) assumes the water uptake of a tree cohort to be controlled by the transpiration demand, the relative amount of fine roots of a tree cohort in a specific soil layer relative to the total amount of fine roots in this soil layer, the available water above the wilting point W_s^{WP} , and a reduction function (Chen, 1993). The reduction function f_{res} is based on the assumption that optimal water uptake only occurs if water content W_s is in range of 10% of the field capacity W_s^{FC} (equation 2.14 in chapter 2). Hence, WU1 follows a demand-approach which looks stepwise from the upper to the lower soil layer for required amount of water. The water demand of a tree cohort is calculated from the potential evapotranspiration and the canopy conductance with regard to photosynthesis. This demand is met by the supply of soil water, calculated from water content of the soil layers reduced by a water content dependent reduction factor (Fig. 2.4). The second approach for water uptake (WU2) was developed by (Campbell, 1991) and describes the water uptake process along a soil-plant-atmosphere-continuum (SPAC). The

proposed algorithm has been implemented in *4C* to simulate water uptake based on the water potential gradient between leaf and soil analogous to electricity flow. The water flows from soil through xylem into the leaves and evaporates through the stomata into the atmosphere. In Fig. 2.4 only the simulated time dynamic components within the applied water uptake approach are illustrated. Two major resistances in the system are calculated: the soil resistance and the root endodermis resistance. Axial resistances within roots and xylem resistances within the stem are not considered in the model and the leaf resistance is constant over time and tree species. The potential gradient with the lowest water potential in the leaves and the highest water potential in the soil is the driver of the water flow in trees. The root resistance in a soil layer is inversely proportional to the relative length of fine roots in that layer. We calculated water uptake with low, medium and high total root resistance (Tab. 4.1). The soil water potentials were calculated on the base of pedotransfer functions from the actual water content (VanGenuchten, 1980).

Forest stands and site conditions

The simulation experiments were conducted on four different forest sites in Germany. We choose two mono-species Scots pine (*Pinus sylvestris* L.) stands (P1, P2) and two mixed Scots pine-oak (*Quercus petraea* [Matt.] Liebl.) stands (M1, M2) located in the lowlands of northeastern Germany. Both mono-species sites are part of the network of long-term forest monitoring sites within the ICP Forest program of the UN-ECE. For the short-term validation we accessed initialization data for the P1 and P2 stand from an earlier investigation in 1994 (Tab. 4.2). The simulation period for long-term validation starts in 1951. Since there were no observed stand data for the start year of simulation in 1951 we used available data of inventories

Table 4.1: Parameter list for water uptake model 2 (WU2).

parameter	symbol	unit	value	source
species specific root length	l_{SRL} (pine)	$m g^{-1} DW$	15	(Hornschuch et al., 2007)
	l_{SRL} (oak)	$m g^{-1} DW$	30	(Hornschuch et al., 2007)
density constant for sandy soil	n	-	1.6	(Campbell, 1991)
air entry potential	ψ_e	kPa	-0.34	(Campbell, 1991)
critical leaf water potential	ψ_c	kPa	-2500	this study
total leaf resistance	R_L	$m^4 kg^{-1} s^{-1}$	$2.2 \cdot 10^6$	(Campbell, 1991)
total root resistance	R_r^{tot}	$m^4 kg^{-1} s^{-1}$		this study
low			$4.0 \cdot 10^6$	
medium			$9.0 \cdot 10^6$	
high			$4.0 \cdot 10^7$	

from 2006 (M1, M2) and 2004 (P1, P2) to generate stands for 1951 from yield table data. We assumed stability in the site quality index (mean dominant tree height at age 100) and in the fraction covered by the two tree species in mixed stands. We initialized the stands on the base of tree age, mean height and mean diameter from the yield table (Tab. 4.2). Soil data were available from soil inventories. The soil characteristics differ between the pure and the mixed stands. Especially the sum of plant available water is much greater for the mixed stands (Tab. 4.3).

Climate data

The climate data are provided by climate stations which are located nearby the forest stands. These climate data include daily measurements of weather parameters

Table 4.2: Stand data for initialization in 1951 and 1994, respectively (d_{bh} =mean tree diameter at breast height, h_g =mean tree height).

site	species	1951				1994			
		age [year]	d_{bh} [cm]	h_g [m]	stock [m ³]	age [year]	d_{bh} [cm]	h_g [m]	stock [m ³]
P1	pine	18	9.0	13.7	209	62	29.8	25.9	458
P2	pine	29	10.5	14.0	205	73	28.3	24.3	347
M1	pine	85	31.8	25.0	258				
M1	oak	85	20.9	20.0	136				
M2	pine	65	24.8	23.1	159				
M2	oak	70	21.2	22.4	239				

Table 4.3: Soil characteristics from soil inventory (W_s^{FC} = Sum field capacity, W_s^{PAW} = Plant available water at maximum rooting depth, C/N = C/N ratio total soil, p_s = range sand fraction, p_c = range clay fraction).

site	soil type	soil depth [m]	W_s^{FC} [mm]	W_s^{PAW} [mm]	C/N [-]	p_s [%]	p_c [%]
P1	brunic arenosol	270	217	119	22	90-100	0-5
P2	brunic arenosol	255	237	93	21	50-100	0-17
M1	brunic arenosol	308	526	369	21	91-98	1-4
M2	brunic arenosol	305	607	395	15	75-97	2-9

(temperature, precipitation, radiation, air humidity, vapor pressure, wind velocity) from 1951-2006 (Tab. 4.4). In case of the pure pine stands (P1, P2) also climate data of a mobile climate station next to the forest stand was available. Here we merged the long time series of the permanent climate station with the short but more precise one of the mobile climate station. The mobile climate station database provides daily measurements of the already mentioned weather parameters from 1996-2004. The climate conditions at the forest sites represent the subcontinental climate prevailing in Brandenburg with low precipitation in the growing season. The

Table 4.4: Location and distance of forest sites and permanent climate station (stand/station).

site	latitude [<i>decimal</i>]	longitude [<i>decimal</i>]	elevation [<i>m a.s.l.</i>]	distance [<i>km</i>]
P1	53.14/53.15	13.04/12.97	75/62	4.8
P2	52.16/52.22	14.12/14.02	75/98	9.5
M1	52.85/52.87	12.18/11.98	48/24	13.6
M2	52.21/52.17	14.48/14.25	73/43	15.8

Table 4.5: Climatic characterization of forest sites on the base of permanent climate stations for 1951-2006 (T_y = mean annual temperature, T_g = mean temperature of growing season (April-September), P_y = mean annual sum of precipitation, P_g = mean sum of precipitation in growing season (April-September)).

site	T_y [°C]	T_g [°C]	P_y [mm]	P_g [mm]
P1	8.1	13.8	600	344
P2	8.5	14.7	550	309
M1	8.5	15.2	531	255
M2	8.9	16.2	521	267

sites slightly differ in the precipitation sum and mean temperature values (Tab. 4.5).

Measured data

Xylem sap flow data Tree canopy transpiration was estimated by sap flow measurements in 10 representative pine trees of stand P1 using the constant heating method. The method is described in detail by (Lüttschwager et al., 1999). The stand sap flow was calculated as the product of average sap flow density and stand sapwood area that was estimated by stand inventory and sapwood area in the sample trees. The measurements were taken from June 1998 until October 1999. The ag-

gregated stand transpiration from the measured data was compared with simulated stand transpiration.

Soil water content The volumetric soil water content was calculated using the time domain reflectometry (TDR) measurements at the P1 and P2 sites. The TDR tubes were installed in three different soil depths (P1: 20, 70, 250cm and P2: 20, 50, 250cm). The observation period lasted from 1997 until 2004.

Tree ring data The growth dynamics of the trees was measured on the base of annual ring widths taken from increment cores. In each case two increment cores were extracted from 20 dominant pines and 20 dominant/subdominant oaks at the M1 and M2 sites in 2006 (Schröder et al., 2009). At P1 and P2 only average annual ring width time series until 2004 for dominant pine trees were available (Beck, 2009). Therefore, the comparison between simulated and measured ring widths was accomplished with the average annual ring width time series also at the mixed forest stands M1 and M2.

Validation procedure The validation of the different model approaches to simulate water uptake were executed with different variables available from the different measurement periods. The processes that are important for tree growth are simulated at different time scales. The soil water balance is simulated with a daily time step and consequently the validation is also done with daily data. The short-term validation with the transpiration measurements on P1 encompasses one and a half year and the soil water measurements on P1 and P2 eight years. The annual diameter increment is simulated at the end of the year when the carbon is allocated to the stem. Therefore, the long-term validation is executed with annual data with

the tree ring chronologies from 1951-2004 (P1, P2) and 1951-2006 (M1, M2) respectively. The average annual ring increment for each species and site were used to derive index series through normalization. The index values were calculated in two steps. Firstly, an autoregressive model converts increment values into index values:

$$I'_t = \frac{rw_t}{(a + b \cdot rw_{t-1})} \quad (4.1)$$

where rw_t is the ring width and rw_{t-1} is the ring width of previous year, a and b are empirical parameters. Secondly, a linear regression minimizes the tree age impacts:

$$I_t = \frac{I'_t}{(a + b \cdot t_{age})} \quad (4.2)$$

where t_{age} is the tree age. We compared the index time series of simulated and observed diameter growth by considering four criteria. The first criterion is the Pearson correlation coefficient r :

$$r = \frac{\sum_{i=1}^N (X_i - \bar{X})(Y_i - \bar{Y})}{\sqrt{\sum_{i=1}^N (X_i - \bar{X})^2 \cdot \sum_{i=1}^N (Y_i - \bar{Y})^2}} \quad (4.3)$$

where X_i is the i th simulated value ($i = 1, \dots, N$), \bar{X} is the arithmetic mean of simulated values, Y_i is the i th measured value ($i = 1, \dots, N$), \bar{Y} is the arithmetic mean of measured values.

The sensitivity index (SI) indicates the year-to-year fluctuations of ring widths (Beck, 2009). Sensitivity index is calculated using the following equation:

$$SI = \sum_{i=2}^N \frac{(x_{i-1} - x_i)}{(x_{i-1} - x_i) \cdot 0.5} \quad (4.4)$$

The third criterion is the "Gleichläufigkeit" score G_{xy} of two tree ring index series x_i and y_i ($i = 1, \dots, N$) and is defined:

$$G_{xy} = \frac{1}{N-1} \sum_{i=2}^N \text{sign}(x_i - x_{i-1}) \cdot \text{sign}(y_i - y_{i-1})$$

with

$$\text{sign}(z) = \begin{cases} 1 & \text{if } z > 0 \\ 0 & \text{if } z = 0 \\ -1 & \text{if } z < 0 \end{cases} \quad (4.5)$$

This index counts how well the two series have followed each other over the years. The last criterion is a drought index DI to detect marker years with small diameter growth due to water shortage. Following (Schröder et al., 2009), we defined a marker year as a year where the diameter increment of year is at minimum ten percent above or below the increment of the previous year. Thereafter only the lower increments were used to filter out the drought years. Because complex interactions between climate, management and diameter growth can confound the effect of drought, we filtered out years where remarkable low diameter increment should mainly be caused by water shortage. For this filtering a cluster analysis was performed on the base of the variables minimum water content in the soil, climatic water balance of the year and number of ice days ($T_{max} < 0^\circ\text{C}$). At each site the classification of the marker years to three clusters were based on the Euclidean distance. As a result marker years with dry conditions could be separated from marker years with a strong winter and marker years with wet conditions. The resulting drought years (Tab. 4.6) fit well to reported drought years in the northeastern lowlands of Germany. The cluster analysis was conducted with the software package "cluster" available for R

Table 4.6: Resulting drought years for specific sites and species.

site	P1	P2	M1 pine	M1 oak	M2 pine	M2 oak
years	1952	-	-	-	-	-
	1959	-	1959	1959	-	1959
	-	1960	-	-	-	-
	-	-	-	1963	-	-
	1968	-	-	-	-	-
	1975	-	-	-	-	-
	1976	1976	1976	1976	1976	1976
	-	-	1982	1982	-	-
	1983	-	1983	-	-	-
	1989	1989	1989	1989	-	1989
	-	-	1990	-	-	-
	1991	1991	-	-	1991	-
	1992	-	1992	-	1992	1992
	-	-	-	1996	-	-
	-	-	-	-	-	1999
	-	2003	2003	2003	2003	2003
	-	-	2006	-	2006	-

(R Development Core Team, 2009). The drought index DI is then calculated as the percentage concurrence of observed and simulated drought years.

Statistical Analysis

To find an overall result of the performance of the water uptake approaches related on the annual diameter increment we combined the four criteria described above. Since all four criteria can be assessed by a scale from 0 to 100%, they were standardized to allow calculating a mean value for the water uptake approaches. Hereby, the standardization of the four criteria is as follows:

$$\text{criteria I} \quad r^* = r \cdot 100 \text{ (if } r < 0; r^* = 0)$$

$$\text{criteria II} \quad G_{xy}^* = G_{xy}$$

$$\begin{aligned} \text{criteria III} & \quad SI^* = 100 - (\|SI_{sim} - SI_{meas}\|)/SI_{meas} \cdot 100 \\ \text{criteria IV} & \quad DI^* = DI \end{aligned}$$

The asterisk indicates the standardized criterion and a value of 100% means perfect compliance with the criterion of the measured index time series. The Tukey test (Lozán and Kausch, 2007) is used to test for significant differences between the four average compliance values of the four water uptake approaches WU1, WU2-low, WU2-medium, and WU2-high. It is a nonparametric test for multiple comparisons that gives a critical difference (D_k) for a level of significance (in this case $\alpha=5\%$). If the difference between two mean values is larger than the critical difference of the Tukey test, then there is significance:

$$\begin{aligned} D_k & = \sqrt{\frac{M_S}{N} \cdot q_{k;v;\alpha}} \\ \text{with} & \\ M_S & = \frac{\sum_{j=1}^k \sum_{i=1}^N (x_{ij} - \bar{x}_j)^2}{(N - k)} \end{aligned} \quad (4.6)$$

where N is the sample size, k is number of samples, x_{ij} is the i th residual of sample j , \bar{x}_j is the mean residual of sample j , q is the value from the studentized range table, v is degrees of freedom, α is level of significance.

The performance of the water uptake approaches simulating stand tree transpiration and soil water content at a specific soil depth was evaluated using the coefficient of determination R^2 between simulated and measured values. The coefficient of variation (CV) as the ratio between the standard deviation and the mean value was calculated to compare variation in simulated and observed soil water content. The statistical analyses were conducted with the specified equations that are im-

plemented in $4C$ and with the statistical software R version 2.10.0 (R Development Core Team, 2009).

4.3 Results

Daily xylem sap flow

The simulated daily stand transpiration rates with WU1 are higher than the observed stand transpiration from the xylem sap flow data. The transpiration simulated with WU2-medium was closest to the simulated transpiration with WU1. The simulation with WU2-high leads to a decrease in transpiration that is lower than observed transpiration (Fig. 4.1). There is a general overestimation of daily tran-

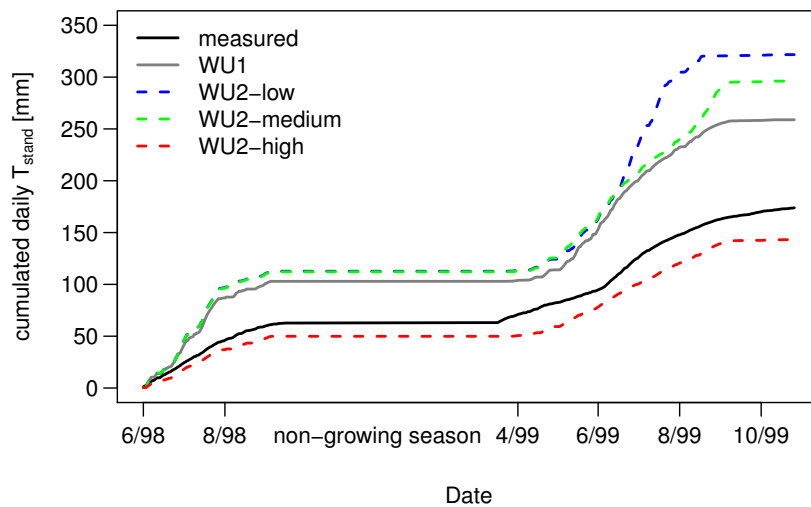


Figure 4.1: Measured and simulated transpiration (cumulated) of P1 site. Simulated transpiration with WU2 involves three different values for root resistance (low, medium, high).

spiration for WU1, WU2-low, and WU2-medium by roughly twice of the observed

values. The correlation between observed and simulated is in all cases around 0.7. The WU2 with high root resistance reduces maximum daily transpiration at a value that is closer to the observed values. The scatter plot also shows that there are a lot of days where no transpiration is simulated but measured (Fig. 4.2).

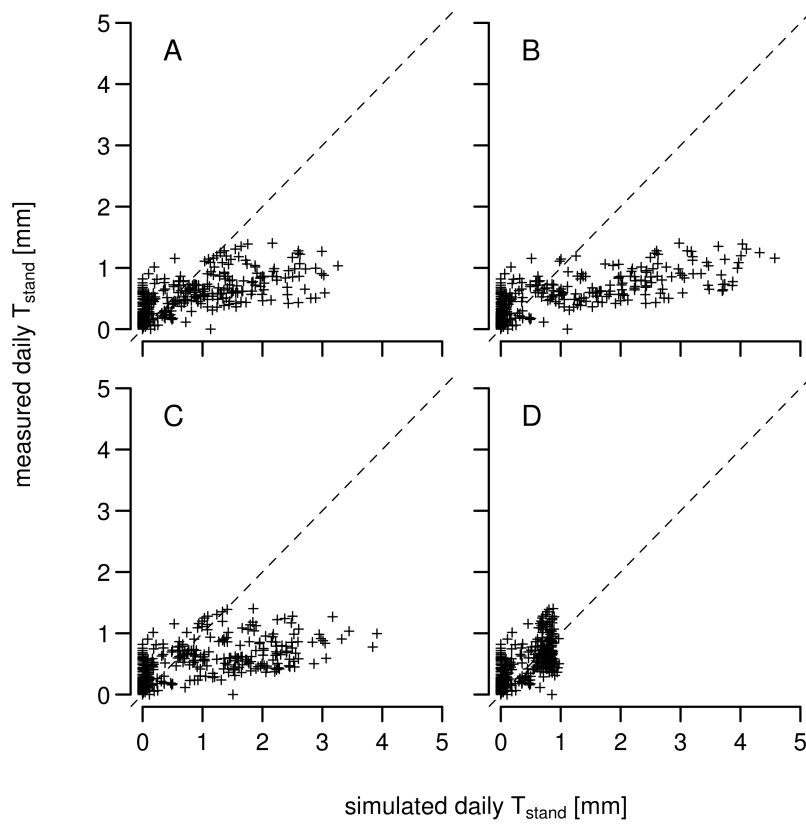


Figure 4.2: Measured and simulated daily transpiration at P1 site for all both water uptake approaches and root resistances from June 1998 until October 1999 (A=WU1, B=WU2-low, C=WU2-medium, D=WU2-high).

Table 4.7: Statistical analyses between mean simulated and observed volumetric soil water content from 1997-2004 at P1. CV is the coefficient of variation, W_s soil water content [%].

	soil depth [cm]	R^2	mean W_s		CV of W_s	
			simulated	measured	simulated	measured
WU1	20	0.50	14.75	15.32	0.17	0.23
	70	0.41	9.95	10.90	0.12	0.11
	250	0.55	8.55	11.88	0.12	0.25
WU2-low	20	0.51	14.37	15.32	0.23	0.23
	70	0.35	9.82	10.90	0.14	0.11
	250	0.36	7.56	11.88	0.38	0.25
WU2-medium	20	0.52	14.57	15.32	0.20	0.23
	70	0.38	9.97	10.90	0.12	0.11
	250	0.31	8.36	11.88	0.23	0.25
WU2-high	20	0.32	15.65	15.32	0.10	0.23
	70	0.43	10.43	10.90	0.08	0.11
	250	0.07	9.15	11.88	0.07	0.25

Daily soil water content

The comparison between observed and simulated soil water content on the base of the R^2 coefficient showed the best agreement of WU1 regarding all three soil depths at P1 (Tab. 4.7). However, the variation in the soil water content in 250 cm soil depth is much lower than observed. The opposite applies for WU2 with low and medium root resistance. The R^2 value is mostly lower than with WU1 but the CV value is higher (WU2-low and 250 cm soil depth) or close to the observed values. The WU1-approach led to water sampling that fitted well to the observed water content measurements in its general pattern (Fig. 4.3 A,B). As observed the water content in upper soil layers is much lower in relative dry years (e.g. 1999 and 2003). This is accompanied by a sharper decrease of water content in the deeper soil layers. However, the magnitude of this decrease is lower than observed which

causes a much lower variation than the observed variation of soil water content. In the upper soil layers there were remarkable differences in the refilling time of both water uptake approaches in comparison to observed data (Fig. 4.3 A,B). After water depletion the simulated soil water content is increasing much more rapidly than the observed soil water content. The results in water content of the upper soil layer with WU2 and a low root resistance were similar to the results of WU1. Though, the simulated minimum soil water content of the upper soil layers in a year is lower than the observed water content and also lower than simulated with WU1 (Fig. 4.3 C). There was a big difference between simulated and observed water content in the deeper soil layers where the model simulated that almost all water could be extracted by the trees in dry years (Fig. 4.3 D). With medium root resistance the simulated soil water content in upper soil layers is closest to the observed values in comparison to all other simulations (Fig. 4.3 E). In deeper soil layers WU2-medium lead to years with almost no water extraction and subsequent lower variation in water content. In the relative dry year 2003 almost all of the stored water was extracted (Fig. 4.3 F). The WU2 with high root resistance lead to lower transpiration and therefore to higher water content in the soil. In the upper soil layers the simulated soil water content is higher than the observed water content in the growing season and the simulated water content with WU1 (Fig. 4.3 G). There was a big difference between simulated and observed water content in the deeper soil layers where almost no water is extracted by the trees in the model simulation (Fig. 4.3 H).

Annual and tree ring data

The mean annual drought reduction factor R_{drind} was lower if water uptake was simulated with WU2 (Fig. 4.4). That means, the highest reduction in photosynthesis due

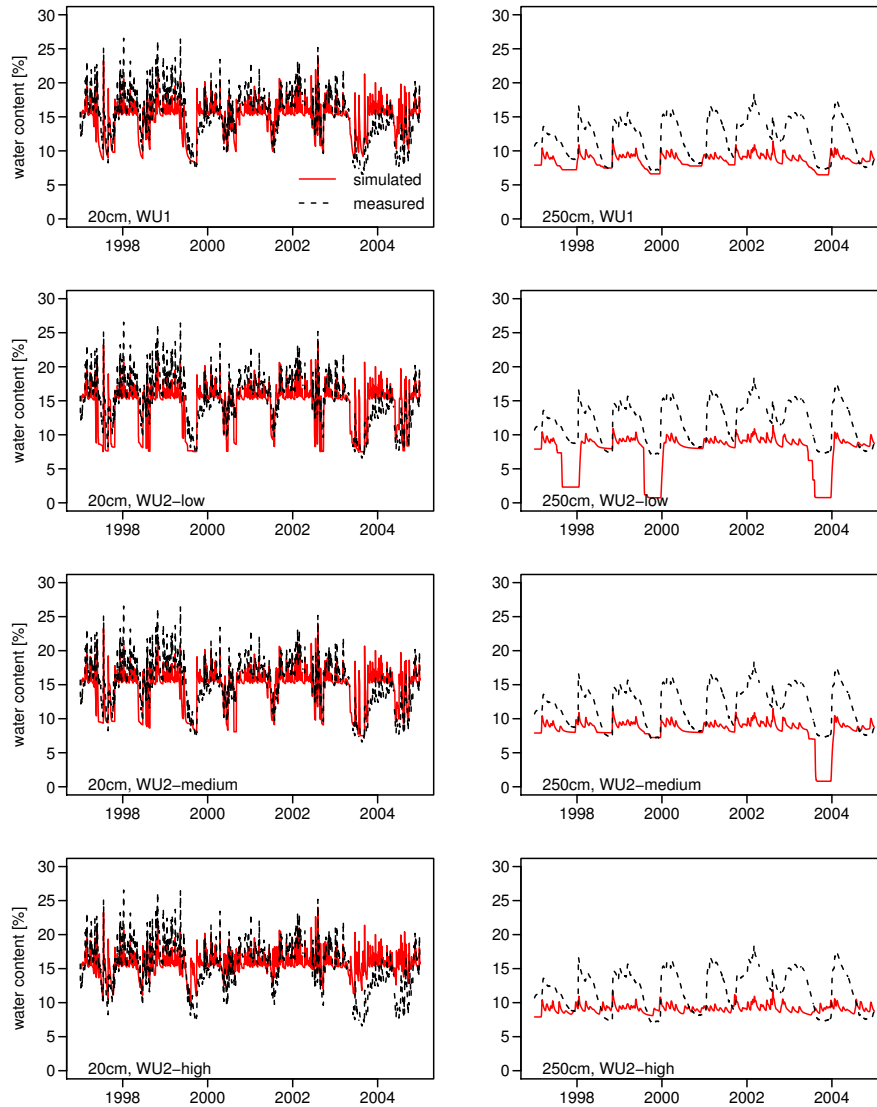


Figure 4.3: Volumetric soil water content at P1. The figure shows daily data for the upper soil layer (left; 20 cm) and lower soil layer (right; 250cm). (A, B=WU1; C, D=WU2-low; E, F=WU2-medium; G, H=WU2-high).

to water stress occurs with WU2-high. The comparison of simulated and observed diameter growth on the base of the index time series offered a more differentiated

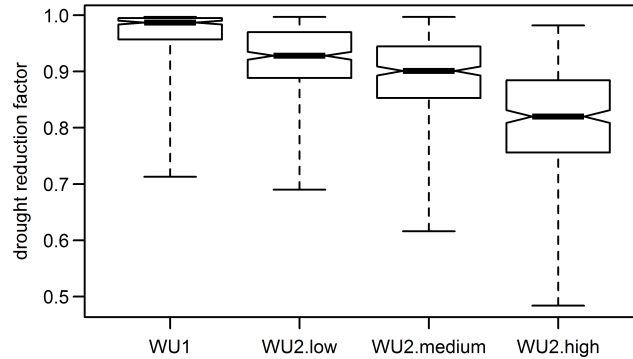


Figure 4.4: Box plots (lower whisker=lowest extreme, lower hinge=first quartile, median, upper hinge=third quartile, upper whisker=highest extreme, the notch represents the standard error of the median (McGill et al., 1978) of the mean annual drought reduction factor R_{drind} in $4C$ over all sites and tree species for the different water uptake approaches. The time period of the average was from 1951-2006 (M1, M2) and 1951-2004 (P1, P2), respectively.

picture. The four assessment criteria show a general trend to better performance of WU2 (Tab. 4.8). At most sites either WU2-medium or WU2-high lead to the highest standardized criteria values. Compared over all sites and standardized criteria the WU2 with high root resistance had the highest mean compliance. The Tukey test calculated a significant different mean compliance for WU1 and WU2-high (Tab. 4.9).

4.4 Discussion

Water uptake and root resistance

The assumed total root resistances of $4.0 \cdot 10^6$, $9.0 \cdot 10^6$ and $4.0 \cdot 10^7$ [$m^4 s^{-1} kg^{-1}$] were set according to the value of $4.6 \cdot 10^6$ which was used by (Campbell, 1991) for tomato plants. For a better comparison of literature root resistance values and

Table 4.8: Comparison of the four different water uptake models on the base of standardized tree ring indexes

site	species	model	r^*	G_{xy}^*	SI^*	DI^*
P1	pine	WU1	37.9	63.5	55.7	66.7
P1	pine	WU2-low	53.4	69.2	90.0	77.8
P1	pine	WU2-medium	55.9	69.2	88.4	88.9
P1	pine	WU2-high	43.2	67.3	95.7	77.8
P2	pine	WU1	29.5	65.4	59.5	66.7
P2	pine	WU2-low	30.5	61.5	12.6	83.3
P2	pine	WU2-medium	30.4	63.5	20.6	83.3
P2	pine	WU2-high	32.8	71.2	14.3	83.3
M1	pine	WU1	14.8	51.9	46.4	0.0
M1	pine	WU2-low	36.9	51.9	42.6	11.1
M1	pine	WU2-medium	48.3	63.0	36.4	22.2
M1	pine	WU2-high	36.5	68.5	45.8	33.3
M1	oak	WU1	25.2	48.1	55.9	42.9
M1	oak	WU2-low	36.9	48.1	56.5	42.9
M1	oak	WU2-medium	33.0	61.1	62.9	71.4
M1	oak	WU2-high	41.1	63.0	94.1	85.7
M2	pine	WU1	14.5	57.4	49.4	0.0
M2	pine	WU2-low	12.5	61.1	43.0	40.0
M2	pine	WU2-medium	34.2	68.5	54.6	60.0
M2	pine	WU2-high	38.8	63.0	72.5	60.0
M2	oak	WU1	6.7	57.4	40.1	50.0
M2	oak	WU2-low	0.0	42.6	54.6	16.7
M2	oak	WU2-medium	8.6	59.3	86.2	50.0
M2	oak	WU2-high	37.3	64.8	78.3	100

Table 4.9: Mean compliance of index value comparison. Asterisk indicates significance ($p < 0.05$).

model	mean compliance
WU1*	42.17
WU2-low	44.51
WU2-medium	55.26
WU2-high*	61.48

our values we converted all values to total root resistance per tree (see chapter 2). The estimated total root resistance of our study ranges from $2.3 \cdot 10^4$ to $2.3 \cdot 10^5$ [$MPa \ s \ m^{-3}$]. The values derived from Coners (2001) and Williams et al. (2001b) are $1.8-8.7 \cdot 10^4$ and $2.5 \cdot 10^5$ [$MPa \ s \ m^{-3}$], respectively. Hence the assumed three total root resistances of our study are in the possible range of forest trees. In our study this parameter showed a high sensitivity. However, due to the complexity of physical and chemical processes which control the root resistance and missing fine root data it was not possible to select a "best" value for our model study.

Short-term root water uptake approach performance

At the daily level there were large discrepancies between simulated and observed cumulated transpiration measured by the sap flow method (Fig. 4.1). According to Kostner et al. (1996) they cannot be explained by the estimation error in the aggregation of transpired water from single tree to the stand since this estimation error does not exceed 10 percent with ten investigated trees in an even aged mono-specific stand. On the other hand Wilson et al. (2001) reported much lower values of stand transpiration measured by the sap flow method than by eddy covariance and water catchment methods. They explained the discrepancies with scaling errors of instrumented trees to the stand due to diversity in stand species composition and ring porous trees. Therefore in case of P1, the sap flow method should give reliable values for tree transpiration but with some uncertainty about the tendency to underestimate transpiration. Some problems occurred with days where no transpiration was simulated but measured (Fig. 4.1) which can be explained with the delay in the beginning of transpiration in the year 1999. The higher root resistance in WU2-high led to lower daily tree transpiration rates with a maximum of 1 mm per day (Fig.

4.2 D). Furthermore, measured daily transpiration values did not exceed 1.5 mm and were seldom above 1 mm. In comparison to other reported maximum values around 3-4 mm per day (Bittner et al., 2010; Granier and Loustau, 1994; Lundblad and Lindroth, 2002) the simulated values with WU2-high as well as the measured values seem to be too low. In contrast to the overestimated transpiration by WU1 and WU2-low the simulated water content were close to the observed water content for these approaches for all soil depths (Tab. 4.7, Fig. 4.3 A-D) Especially, the soil water content of the lowest layer (250 cm depth) was simulated with the same intra-annual pattern of a water content decrease during summer and a clear increase during winter time. In WU1 this is obviously caused by the water demand and the ability of the approach to satisfy this demand with the water from all soil layers. In the case WU2-low the water supply was not limited due to low root resistance in this layer. Vice versa, since lower tree transpiration was simulated by WU2-medium and WU2-high, the soil water content was much higher than observed (e.g. Fig. 4.3 E-H). During the very dry and heat summer of 2003 WU2-high simulated a higher water content than measured in the upper soil layer (Fig. 4.3 G). Also in the lowest soil layer the simulated soil water content did not show the seasonal pattern of variation. This was caused by the high root resistance which in combination with low root length density led to a high limitation in water uptake. These findings may lead to the conclusion that the approach which described transpiration in the best way did not meet the measured soil water content and vice versa. This result can be explained by missing soil vegetation transpiration in the stand transpiration measurement. According to Lüttschwager et al. (1999) soil vegetation participates with 30-40% to the total stand transpiration in similar pure pine stands. *4C* simulates soil vegetation as a simple species independent leaf-area layer

and its fraction of the total stand transpiration was in each case smaller than 10 % (data not shown). The result was an underestimation of simulated soil vegetation transpiration. If soil vegetation would be more realistic the tree transpiration would drop and simulated transpiration of WU1, WU2-low and WU2-medium would be lower. WU2-high would not drop much since still soil water is available. However higher soil vegetation transpiration would decrease the soil water content. Thus, make WU2-medium and WU2-high more realistic with regard to soil water content measurements.

Impact of Root water uptake approach on diameter growth

At the annual level, considering tree ring data, there was a general trend to a better performance of the WU2 approach. On the base of the mean compliance over all criteria the best results were found with WU2-high (Tab. 4.9). In this case the average drought reduction factor R_{drind} had the lowest values (Fig. 4.4) and additionally, the drought index DI, the correlation and the Gleichläufigkeit Gxy between the index series reached the highest values for WU2-high or WU2-medium (Tab. 4.8). Lower values of R_{drind} resulted in a higher reduction of net primary production and subsequently of the diameter growth due to drought stress. This corresponds to a better correspondence between observed and simulated drought years, indicated by DI. For both tree species and for all sites the sensitivity index (SI) criterion, calculated for the tree rings simulated with WU2, corresponded better to the SI of the measured tree rings in most cases as well (Tab. 4.8). Considering high sensitivity of ring widths as a clear indicator of stress conditions (Beck, 2009) this finding supports the idea that the higher drought stress simulated with WU2 led to a more realistic performance.

The diameter growth of most tree species in the temperate regions is less sensitive to droughts late in the growing season, which is not accounted for in growth models if allocation is simulated with an annual time step (Hanson et al., 2004). $4C$ works with such an annual time step of allocation and this may lead to an overestimation of drought stress impact on diameter growth. A better match of the measured index time series could be achieved if $4C$ would allocate the assimilated carbon at shorter time scales.

There were no significant differences in the criteria between the two tree species and the four sites. This supports the assumption of similar growing conditions at these sites. Here, water availability is a limiting factor for tree growth. It seems that with WU1 the simulated drought reduction factor was not capable to describe the water stress at the sites. WU2 led to higher water stress and better agreement to the measured tree ring index time series depending on the root resistance. This is in accordance with findings that reductions in sap flow over time and resulting drought stress could be best explained by rising soil-root resistance (Williams et al., 2001a,b). However, in our study this does not led to better compliance with measured daily transpiration and soil water content data at the same time.

4.5 Conclusion

Regarding our first question the difference between WU1 and WU2 is mainly the nonlinear relationship between soil water content and soil water potential which determines the soil water resistance. This induces different results in root water uptake of WU2 in comparison to WU1 which is linearly dependent on the soil water content reduction factor. The study also showed also the high influence of the

assumed total root resistance on water uptake. In WU1 modeled root distribution and consequently root length densities in different soil layer have negligible effects on water uptake. In contrast the modeled root length densities lead to high limitations in water uptake of WU2 with high total root resistance. Concerning the second question we found the highest compliance between observed and simulated drought years by the WU2 approach with high total root resistance. Referring to the last question this study did not identify an approach which performs best regarding all three validation data sets. For a better validation of both approaches it is necessary to include measurements of root length densities and water uptake rates of fine roots on the same site. However this study clearly indicates that forest process-models aiming at simulating drought conditions require validation of different processes and time scales. Further it revealed the importance of a realistic modeling of soil vegetation transpiration especially in mature pine stands with high soil vegetation cover.

Chapter 5

Management of mixed oak-pine forests under climate scenario uncertainty

5.1 Introduction

Pure pine stands dominate the forest of the north-eastern lowlands in Germany. Similarly to recent forest conversion trends in other parts of Europe (Zerbe, 2002), they are converted into mixed stands. One main problem in the analysis and planning of forest management in mixed stands stems from the lack of knowledge about the future climatic development. Therefore, recent studies established conceptual frameworks to evaluate forest management strategies under climate change (Prato, 2008b,a; Seidl et al., 2011). They highlight the importance of considering potential risk and uncertainties from changing environmental conditions as a basis for forest management strategies. Prato (2008b) defines four steps in his framework for assess-

ing ecosystem impacts of climate change: (1) determining the acceptability of the current state of the ecosystem; (2) specifying climate change scenarios; (3) assessing the ecosystem impacts of the scenarios; and (4) identifying the best adaptation strategies for alleviating unacceptable impacts of the climate change scenarios. In this study the proposed framework was applied at the stand level for multiple reasons: Forest managers have to deal not only with conversion from pure pine forests into mixed forests but also with a shift of the management objectives from timber production to a multifunctional sustainable forest management. Oftentimes, the questions are how silvicultural concepts modify the adaptive capacity of mixed stands to climate change (Reyer et al., 2012) and how to meet the objectives of several stakeholder groups. Carbon sequestration in living tree biomass and high biodiversity at tree species level are in contrast to high diameter increments of tree individuals and short rotation periods for maximizing timber yields. The changing environmental conditions may alter management objectives within one cycle of stand development or even less and are very difficult to predict. In recent years, an increase in demand of woody biomass has been observed and is likely to even increase in the future due to energy policies (Bundestag, 2004; CEC, 2007). Mixed oak-pine forests therefore also have to meet a productivity objective to be an accepted silvicultural alternative to high productive pure pine forest stands.

With this background, the obvious advantage of the proposed framework is its possibility to include the uncertainty of climate change scenarios and different management objectives. In addition, it uses various methods such as the stochastic dominance criterion to rank different management strategies depending on their ability to meet management objectives. The framework can easily be applied for a model-based assessment of management scenarios under climate uncertainty at

a single forest stand: (1) determining the acceptability of the current state of the ecosystem; (2) specifying climate change scenarios; (3) model-based assessing the climate impacts of the scenarios on the forest stand; and (4) identifying the best management scenario for alleviating risks missing management objectives. Step one is not included in this study because of the general high acceptance of mixed oak-pine stands.

Scientific tools to study climate impacts on forest ecosystems are process-based forest growth models (Mäkelä et al., 2000; Landsberg, 2003). We applied the forest growth model *4C* to estimate frequency distribution of model output variables from different management scenarios under several climate scenarios. In this study we specify a simple example of a weighting factor times management objective matrix to evaluate the management scenarios. The output results are aggregated into a total performance index (TPI) to rank different management scenarios. We choose simple management scenarios and management objectives to better distinguish the management and climate effects at the site and to demonstrate the suitability of this method for evaluating forest management alternatives. Therefore, this study strives to answer the following questions: (1) Is the proposed framework an useful method for analyzing climate impact studies at the forest stand level? (2) What are the combined effects of management and climate scenarios on forest production?

5.2 Material and Methods

Forest Stand and Site

We used the process-based forest growth model *4C* to analyze the growth of a mixed oak-pine stand (*Quercus petraea* (Mattuschka) Liebl., *Pinus sylvestris* L.). The oak-

pine stand is a typical example of the ongoing forest transformation on forest sites in the north-eastern lowlands where conditions for beech (*Fagus sylvatica* L.) are not suitable. It is situated in the Federal state of Brandenburg circa 80 km in the south of Berlin (Fig. 5.1) and is located in the transition zone between the oceanic climate of Western Europe and the continental climate of Eastern Europe. The climate in this region is one of the driest within Germany (Tab. 5.1). The relief is mainly even



Figure 5.1: Location of the simulated mixed oak-pine stand in Brandenburg.

und shows only small differences in altitude. The soil characteristics are the result of fluvial and aeolian sedimentation during periglacial processes in the Pleistocene. The stand stocks on a sandy cambisol without access to groundwater. The nutrition level and the water storage capacity are low. In the formerly pure pine forest the

Table 5.1: Forest site characteristics with mean temperature (T) and precipitation sum (P) for the period 1961-1990, C/N carbon-nitrogen ratio, pH -value, base saturation (B_s), plant available soil water storage capacity (W_{PAW}), age of oak and pine trees, mean diameter at breast height (d_{bh}), mean height (h_g) and stem number per hectare (N_{stem}).

group	variabel	values	
climate		year	May-September
	T [°C]	8.3	15.2
	P [mm]	589	291
soil		Oh (3.8cm)	Ah(12cm)
	C/N	23	27
	pH [H_2O]	4.1	3.9
	B_s [%]	42.9	9.6
	W_{PAW} [mm]	-	246
	stand		pine
age		104	9
d_{bh} [cm]		33.5	-
h_g [m]		26.1	1.3
N_{stem} [ha^{-1}]		386	4000

oak trees were planted with a density of 4000 seedling per hectare. The stand data were measured in 2006 and were used for the initialization of the simulated stand (Tab. 5.1).

Climate Scenarios

Climate scenarios enable the analysis of future development of climate conditions and its consideration in forest management planning. In this study we used climate scenarios of the regional statistical climate model STAR 2.0 (Orlowsky et al., 2008). It was developed to calculate future daily weather data from observed weather time series on the base of an assumed temperature trend. Statistical methods combine observed daily weather from the past to new time series which meet the predeter-

mined temperature trend at the end of the simulation period. The fundamental assumption of this modelling technique is that physical boundary conditions do not change during the simulation period until 2060. The climate scenarios are named after their temperature trend (0 K, 2 K and 3 K). One climate scenario includes 100 realisations of such predetermined temperature trend. The realisations of one scenario feature the same temperature trend but the combination of the observed daily weather is different. Accordingly, they show small variation in the mean annual temperature value (Fig. 5.2). However, they differ in their daily values and also in their mean annual values of weather variables like precipitation and total radiation. On the base of these 100 realisations per scenario it is possible to establish frequency distributions of weather variables which express uncertainty within each climate scenario.

Management Scenarios

To account for different management types, three management scenarios (*A*, *B*, *C*) were developed which enables testing the impacts of different thinning grades and consequently stand densities on species-specific tree growth. The thinning interval of five years was held constant over the management scenarios. The thinning intensity increases from management scenario *A* to management scenario *C* (Tab. 5.2).

Model Simulations

The model *4C* was run for the mixed oak-pine stand under the three different management scenarios and for three different climate change scenarios and their respective realisations as described above. The combination of climate scenarios and management scenarios is described in Tab. 5.3. The simulation period covered

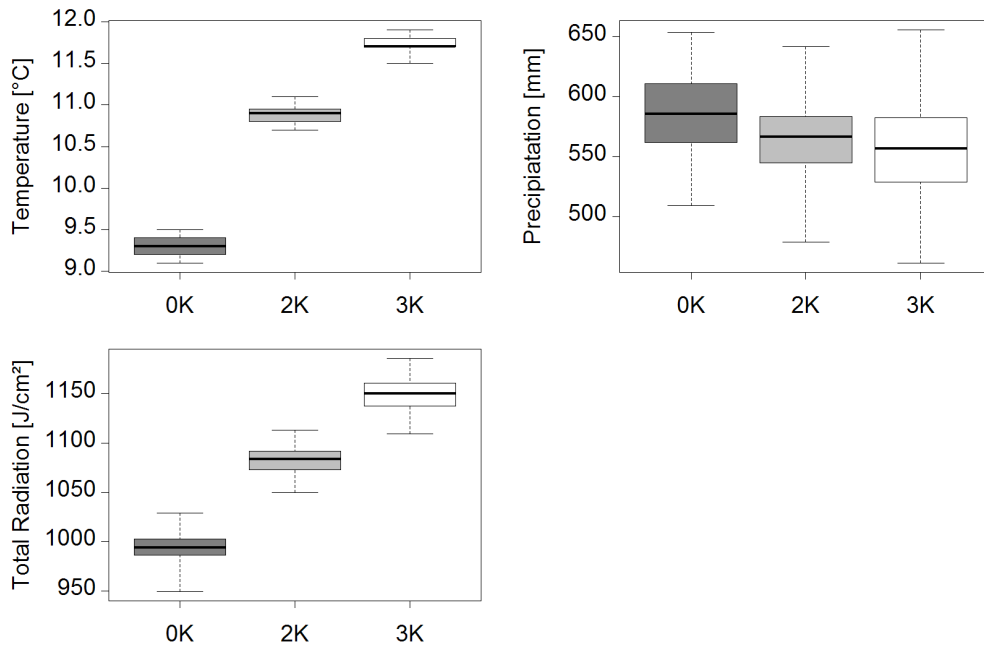


Figure 5.2: Mean values of different climate variables for the three climate scenarios (0 K, 2 K, 3 K) of the period 2036-2060.

Table 5.2: Forest management scenarios used in the analysis with different thinning grades. Numbers represent remaining stems per hectare.

	A		B		C	
year	pine	oak	pine	oak	pine	oak
1	207	-	156	-	117	-
6	192	-	144	-	108	-
11	179	3543	134	3468	101	3393
16	168	3325	126	3183	94	3041
21	159	3115	118	2913	88	2711

25 years from 2036-2060. The simulated output of the stem increment of the total stand was taken to distinguish between climate realisation effects and management effects within a climate scenario. For this reason a bifactorial analysis of variance

Table 5.3: Definition of simulation experiment runs.

management scenario / climate scenario	A	B	C
0K	A-0K	B-0K	C-0K
2K	A-2K	B-2K	C-2K
3K	A-3K	B-3K	C-3K

were performed with the three management scenarios and the 100 climate realisation of one climate scenario.

Multi-criteria Evaluation Concept

To evaluate the management scenarios under climate change, we used the total performance index (TPI) according to Prato (2008b). We selected nine model output variables (Tab. 5.4) as impact criteria. The output variables are linked to three measures which are often used to evaluate management strategies: above and belowground biomass after the simulation period (biomass), sum of annual stem mass increment (growth), and sum of harvested stem wood (harvest). Furthermore, we considered the following management objectives:

- Objective 1: Maximizing carbon sequestration on the site
- Objective 2: An intermediate objective between objective 1 and objective 3 with moderate focus on growth
- Objective 3: Maximizing yield and carbon sequestration in forest products

We defined exemplary weighting factors between 1 and 4 for these management objectives for each output variable according to their different foci to calculate the TPI (Tab. 5.4). The TPI aggregates the normalised output variables of the model

Table 5.4: Weighting factors for three different management objectives.

			objective 1	objective 2	objective 3
biomass	[t DW ha ⁻¹]				
total		w_1	4	1	1
pine		w_2	4	1	1
oak		w_3	3	1	1
growth	[t DW ha ⁻¹]				
total		w_4	4	2	1
pine		w_5	4	2	1
oak		w_6	3	3	1
harvest	[t DW ha ⁻¹]				
total		w_7	1	1	4
pine		w_8	1	1	4
oak		w_9	1	1	4

and is calculated in the following way:

1. Calculation of the maximum $X_{max,j,i}$ ($j = 1, \dots, 9, i = A, B, C$) for each output variable and each management scenario from the set $X_{j,i} = \{x_{j,i}^k, k = 1, \dots, 100\}$ of 100 values $x_{j,i}^k$ resulting from 100 simulation runs.
2. Calculation of maximum values over the three management scenarios:

$$X_{max,j} = \max(X_{max,j,i}) \text{ for } i = A, B, C \quad (5.1)$$

3. Calculation of a set of normalised values $X_{j,i}^n$ for output variable j ($j = 1, \dots, 9$) and management i ($i = A, B, C$)

$$X_{j,i}^n = \frac{X_{j,i}}{X_{max,j}} \quad (5.2)$$

4. Calculation of the TPI for each management scenario i ($i = A, B, C$) as

weighted average:

$$TPI_i = \frac{\sum_{j=1}^9 w_j \cdot X_{j,i}^n}{\sum_{j=1}^9 w_j} \quad (5.3)$$

The values of TPI_i ($i = A, B, C$) were calculated for each of the three climate scenarios. A triangular probability distribution was established with minimum, median and maximum of each set of TPI values from which the cumulative distribution function (CDF) was derived. Using the method of stochastic dominance (Schmid and Trede, 2006) these values were analysed for each management objective, climate, and management scenario. The stochastic dominance is defined as follows: if the value of the CDF of an option B , $F_B(x)$, is less or equal than the value of CDF of an option A , $F_A(x)$, for each value of x , then is option B stochastic dominant of first degree. Figure 5.3 sums up the applied methods and the progression of the working steps.

5.3 Results and Discussion

Simulations

Biomass The total biomass for one management scenario after 25 simulation years is highest under the 0 K scenario, slightly lower under the 2 K scenario and lowest under the 3 K scenario (Fig. 5.4). Much stronger differences in total biomass occur between the management scenarios within each scenario (Fig. 5.4). Management scenario A always yields the highest total biomass (around 450 tDW ha^{-1}), management scenario B yields around 370 tDW ha^{-1} , and management scenario C always ends up with around 310 tDW ha^{-1} . The total biomass at the end of the simulation period heavily depends on the stand growth and on the harvest level during the

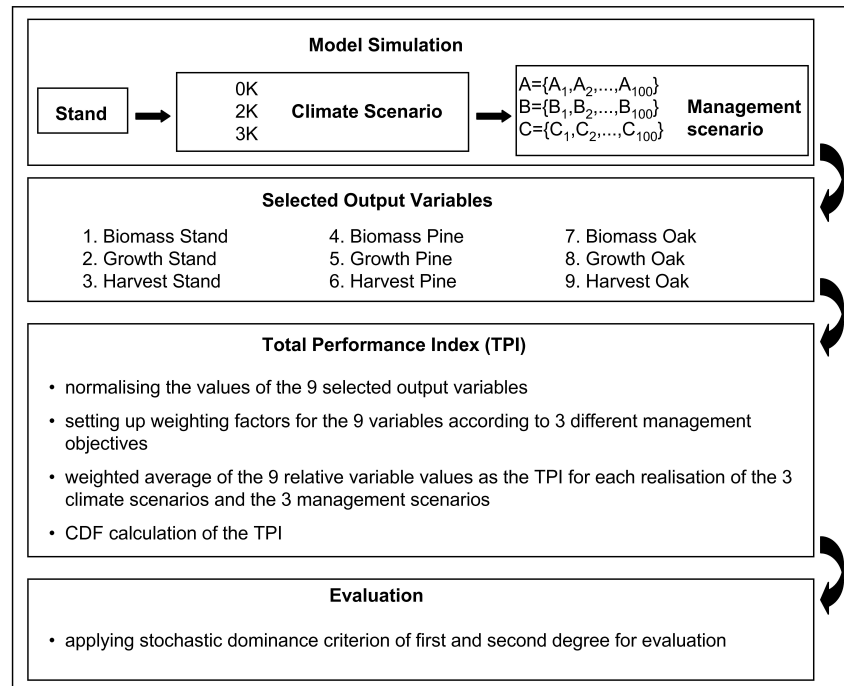


Figure 5.3: Overview of the methodological approach used in this study.

simulation. The decreasing total biomass from management scenario A to C thus reflects increasing management intensity in these scenarios. This is in accordance with results from modeling and experimental studies (Skovsgaard et al., 2006). Although, the effect of the climate scenarios on the total biomass is much less pronounced than the effect of the individual management scenarios, there is still a decreasing trend in total biomass from the 0 K to the 3 K scenario visible. A warmer climate decreases total biomass in all three management scenarios, however, this variation between climate scenarios is much smaller than the variation between management scenarios. This confirms recent climate impact studies which find a much stronger effect of management-related issues such as cutting cycle, age structure of the forest or management history than of climate change in managed European forests (Lindner,

2000).

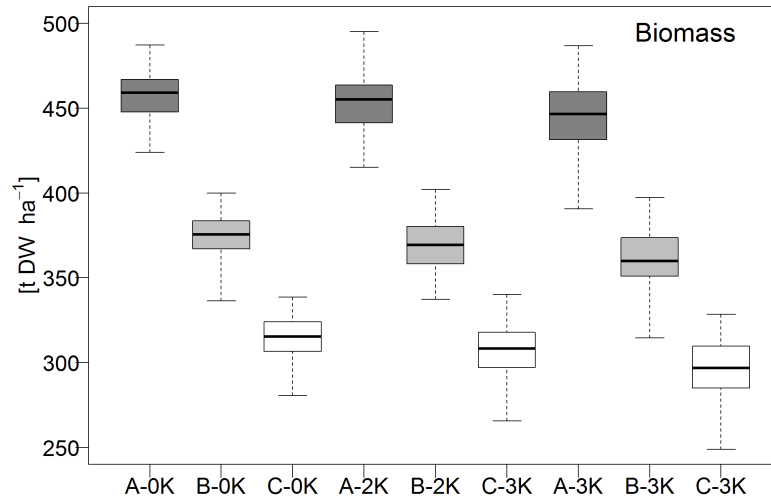


Figure 5.4: Final Biomass for three management scenarios and three climate scenarios. The thick black line denotes the median, the boxes indicate 25 and 75-percentiles, and the Whiskers show sample minimum or sample maximum.

Growth and Harvest The results for stem mass increment show a similar pattern than the total biomass. Across the climate scenarios, increasing management intensity features decreasing stem increment as a consequence of the higher harvest rates and a warmer climate induces lower growth across management scenarios (Fig. 5.5). When considering the harvested stem wood, the pattern among the management scenarios is inverted. With increasing management intensity, the amount of harvested wood logically increases too (Fig. 5.5). However, the amount of harvested stem wood varies only very little in between the different climate change scenarios and the variation around the median is much smaller than for total biomass and biomass growth (Fig. 5.5). Thus, the amount of harvested stem wood is almost independent of the climate. Allocating carbon to the stem comes at the lower end

of the allocation hierarchy in trees (Waring, 1987) and results in lower stem mass increment in years with less favourable conditions. The diameter at breast height is positively correlated with total biomass (Lehtonen et al., 2004) and also with the competitiveness of a tree. Furthermore trees with high growth rates have better access to water and radiation. Since we simulated thinning from above the highest and more competitive tree individuals were harvested first. Hence, trees with less growth variation in the past come to the harvest pool and trees with higher growth variation remain on the site. This explains why the total biomass and growth is more sensitive to changes in climate than the yield.

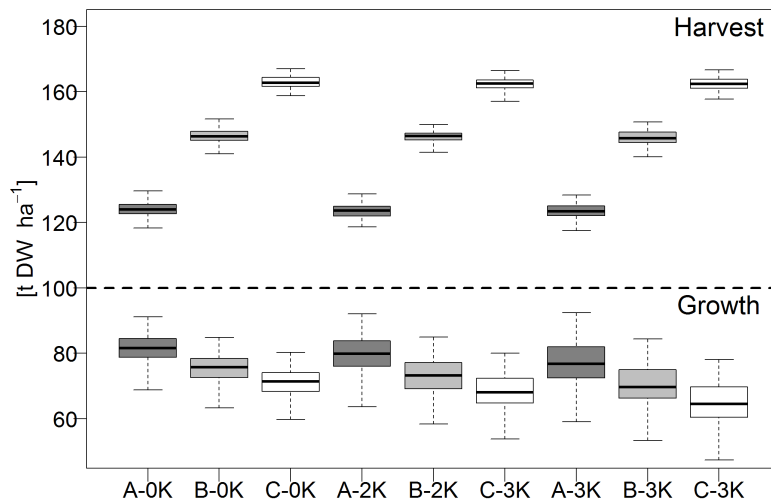


Figure 5.5: Sum of harvested stem wood (above the dotted line) and sum of stem mass increment (below the dotted line) for three management scenarios and three climate scenarios. The thick black line denotes the median, the boxes indicate 25 and 75-percentiles, and the Whiskers show sample minimum or sample maximum.

Effects of management and climate within the climate scenario

To detect the relative contribution of management and climate over 100 realisations to the uncertainty of the simulated stem mass increment within the different climate change scenarios, we calculated the coefficient of variation of management and climate. The warmer climate change scenarios induce a higher coefficient of variation for both climate and management (Fig. 5.6). For the 0K and 2K scenarios, the influence of the climate is lower than the influence of the management but under the 3K scenario the coefficient of variation of the climate is clearly higher than the management one (Fig. 5.6). The increase in influence of the management across the three climate change scenarios is almost linear, whereas the influence of the climate undergoes a step increase from the 2K to the 3K scenario.

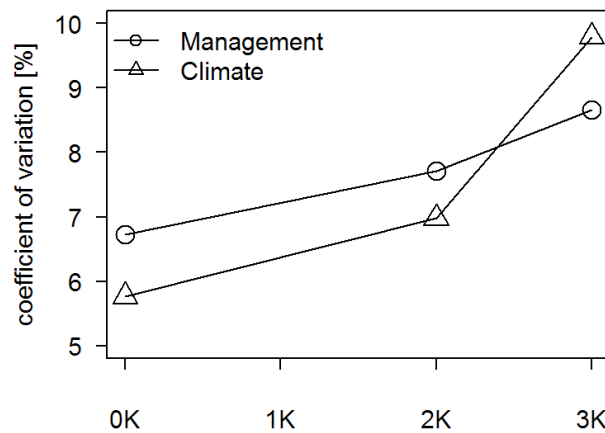


Figure 5.6: Coefficient of variation for the simulated stem mass increment.

Additionally, to the coefficient of variation, we performed a bivariate analysis of variance to track the degree to which the overall variance of stem mass increment can be attributed to the influence of the climate (as expressed by 100 realisations) and of management in the model. Under the 0K scenario both climatic and man-

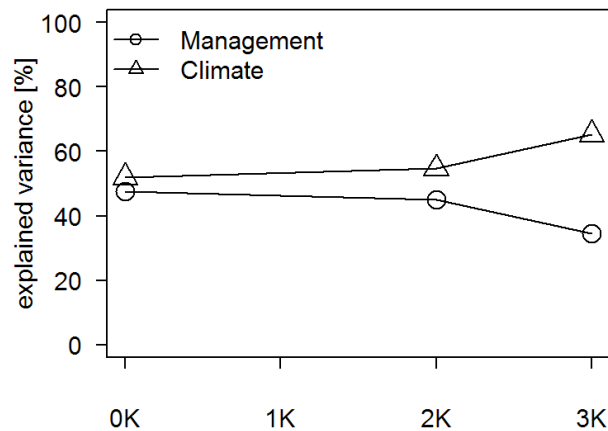


Figure 5.7: Explained variance for the simulated stem mass increment.

agement influence explain about 50% of the variance respectively (note that since management and climate were the only contributing variances in this analysis, they sum up to the total variance i.e. 100%). With increasing warming the influence of the climate increases and the influence of the management decrease (Fig. 5.7). The strongest increase (decrease for management) occurs from the 2 K scenario to the 3 K scenario. This is a noteworthy result because it exemplifies the non-linear dynamics of the climate impacts. Whereas a net temperature increase of 2 K from the 0 K scenario to the 2 K scenario induces only slight changes in the variance explained by the 100 realisations, a further net increase by only 1 K from the 2 K scenario to the 3 K scenario adds about 5% to this variance. The analysis of the coefficients of variation and the analysis of variance show that the climatic uncertainty increases under higher temperatures and its influence may become more important than the management influence in the future. This is especially important since we only simulated stem mass increment without accounting for changes in disturbances such as storms or insects, which are likely to increase (Lindner et al., 2010; Panferov et al.,

2009) and have the potential to increase the influence of the climate dramatically.

Multi-criteria evaluation

The set of weighting factors and management objectives only serve as a simple example to test the methodological approach. In practice a climate impact study who aims analyzing adaptation capacities or adaptation strategies need the participation of stakeholder groups (Prato, 2008b; Seidl et al., 2011). For the first objective, management scenario *A* has the highest probability of reaching a high total performance index across all climate change scenarios (Fig. 5.8). This coincides with the low thinning grade which led to high biomasses of the old pine. The high weighting factors assigned to biomass in objective 1 (Tab. 5.4) supports the TPI of management scenario *A*. Thus, management scenario *A* is most suitable for achieving objective 1. For the second and the third objective, management scenario *C* is most probable to achieve the highest TPI (Fig. 5.8). Similarly to the relationship of objective 1 and management scenario *A*, the results for the third objective coincide with a focus on harvest in management scenario *C* and high weights for harvest in objective *C*. Thus, this confirms the expectations that a management scenario *C* would be most suitable for objective 3. The results for objective 2 deserve closer attention, since this objective balances harvest on the one hand and total biomass and growth on the other hand. Biomass and harvest are not pronounced by the weighting factors, only growth of oak, pine and the total stand are higher weighted. This objective is most likely attained with the strongest management scenario indicating that the losses in total biomass and growth as suggested by the simulation results (Fig. 5.4, Fig. 5.5) in this scenario are compensated by the much higher harvest levels (Fig. 5.5). Furthermore, the lower uncertainty of harvest levels (see **Growth and Har-**

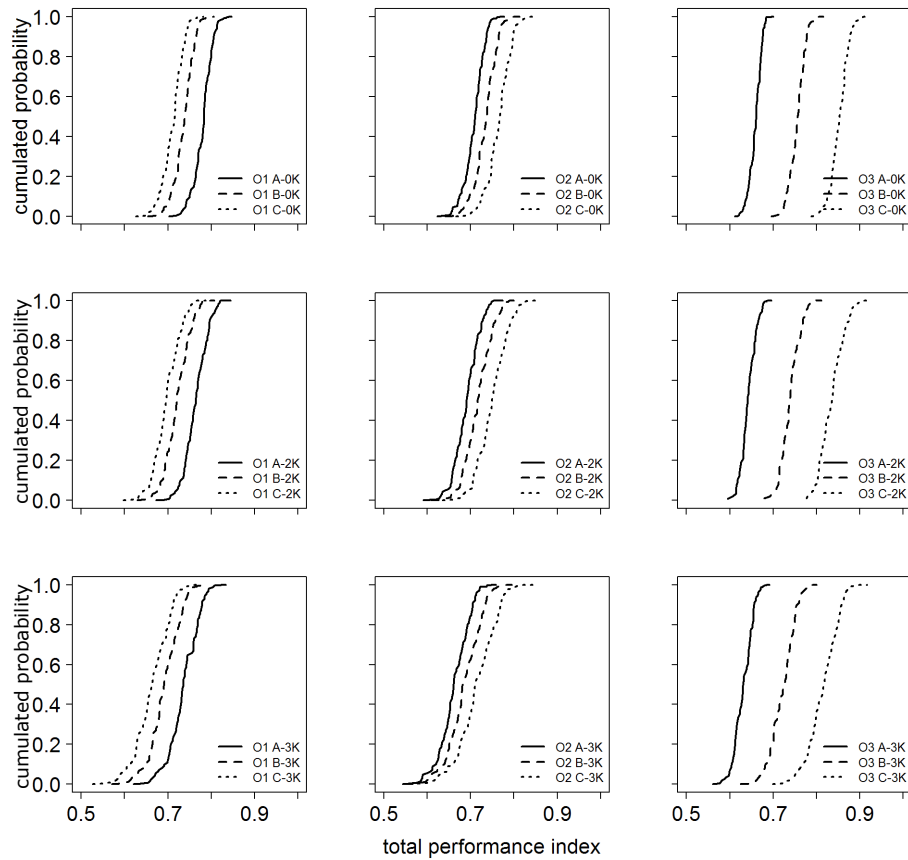


Figure 5.8: Cumulated probability distribution function of the TPI for three management, three climate scenarios and three sets of weighting factors for the management objectives.

vest, page 105) within the 100 realisations explains why management scenario *C* also performs best for objective 2. Additionally, the much less stock of old pine trees in management scenario *C* have positive effects on the growth of young oak trees which is amplified by the weighting factors. Concerning the shape of the CDFs it can be stated that the slope of the CDF is less steep with higher temperature trend which reflects the higher variation (see in section **Effects of management and climate within the climate scenario**). This leads to lower probability reaching

a certain level of TPI but does not change the ranking of management scenarios in this study.

5.4 Conclusion

The conceptual framework developed within this study - the integration of climate and management scenarios, taking into account climate uncertainty and management objectives, and the development of a performance index - is a unique approach in forest sciences. The focus on mixed stands has rarely been investigated; therefore this study is of great importance for foresters. The approach has proven to be highly suitable for the assessment of climate impacts on forest stands.

The analysis of variance of growth related model outputs and the CDFs of the TPI showed an increase of climate uncertainty with increasing climate warming. Interestingly, the increase of climate induced uncertainty is much higher from 2 to 3K than from 0 to 2K. This exemplifies the non-linear impacts of climate change on forest growth.

For future applications of this framework in forest management and forest decision making it is necessary to determine the weighting factors more precisely by involving stakeholders and forest experts.

Chapter 6

Overall Discussion

This chapter comes back on the questions posed at the beginning of my thesis (chapter 1.5). It provides a synthesis of the specific findings of chapter 3-5 and highlights some relevant key issues which are most relevant for future modelling studies from my personal perspective.

6.1 Forest Productivity and Drought Responses

The questions to answer were:

- How does the NPP for the four main tree species of Germany depend on climate factors?
- What are the impacts of climate change on NPP of the four tree species ?
- Which regions in Germany are likely to experience a significant change in NPP?

- How large is the uncertainty of NPP regarding climate scenarios and are there regional differences?

The multiple regression functions reveal strong correlations of simulated mean annual NPP with mean annual temperature, mean annual radiation and the drought index as a value for the duration of periods without rainfall. The relationship between mean annual temperature and NPP fits a logarithmic curve. On the one hand model results show further potential for increasing growth, but on the other hand it reveals a slowing of the increase at higher temperatures. There is an optimum mean annual temperature which could not be detected by this study. But experiments showed clear negative photosynthetic responses of temperate tree species to high temperatures (Dreyer et al., 2001; Dillaway and Kruger, 2010). With the model simulation I detect further a strong linear relationship between radiation and NPP. This is not surprising due to $4C$ -calculated assimilation rates are directly linked to photosynthetically active radiation (PAR) and neglects leaf structural and functional acclimation to irradiance discussed by Sinoquet et al. (2001); Meir et al. (2002); Wyka et al. (2007). Therefore the positive NPP effects based on increased radiation could be biased in $4C$ model results. There is also a strong signal in the NPP results relating on the length of periods without precipitation. If droughts in future become more frequent and its intensity will be more pronounced the NPP in affected regions will decrease. This has been observed already in the past (Breda et al., 2006; Boisvenue and Running, 2006).

The simulated NPP for all tree species increases on the majority of the forest area in Germany with rising temperatures. Especially on temperature limited sites such as mountainous regions or on forest sites with high precipitation high positive NPP changes have been found. However, beyond a 2K temperature slope the SRM-

calculated range of NPP at water-limited forest sites is increased due to different realizations of climate scenarios. Here the results indicate a high influence of precipitation pattern on NPP. There is a general positive relationship between the altitude of a forest site and the percental change and a negative relationship between altitude and the range of NPP due to realizations. The forest production in Brandenburg, where the forest area is always at low elevation, is strongly affected by future precipitation pattern. The uncertainty due to this fact account for up to $1.6 \text{ tC ha}^{-1}\text{a}^{-1}$ of pine stands under a 3K-scenario. This uncertainty decreases in regions where precipitation plays a minor role as a limiting factor of tree growth. Concerning Drought the questions at the beginning of my thesis were:

- What are the effects of using two different water uptake approaches in $4C$ on model behaviour?
- How do simulated results of transpiration and annual diameter increment fit to measured data?
- Is the forest growth model $4C$ able to describe with both water uptake approaches the impacts of extreme weather events like droughts on diameter increment?

Prospective physiological-based modelling studies in water limited regions should include detailed information about vertical distribution of root length densities. Coupled with transpiration or sap flux data the performance of water uptake models within forest growth models can be significantly increased. The main difference between WU1 and WU2 is the non-linear relationship between soil water content and soil water potential which determines the soil water resistance. This induces different behaviour in root water uptake of WU2 in comparison to WU1 which is

linearly dependent on the soil water content whereas WU2 also depend on the root length densities. In WU1 modelled root distribution and consequently root length densities in different soil layer have negligible effects on water uptake. Although it is conceivable to develop also an empirical relationship between water uptake and root length density I would suggest further precise studies with WU2 where modelled root resistances and soil water potentials can be validated by measured data along the soil-plant-atmosphere continuum. I found the highest compliance between observed and simulated drought years by the WU2 approach with high total root resistance. The accordance is between 33 and 100 % depending on simulated forest stand. The model proved to be a suitable tool for assessing drought related risks of mixed oak-pine forest stands. However, this study did not identify an approach which performs best regarding all three validation data sets. Daily simulated variables as soil water content and stand transpiration fit poorly to measured data. Also the correlation between measured and simulated index time series of diameter increment is not higher than 0.56. This lack of accordance at the overall view of carbon and water cycle within the forest stands does not allow a more detailed quantification of future drought risks for pine and oak trees as the more general approach of chapter 3. In addition, until the role of increasing atmospheric CO₂-concentration with respect to water uptake efficiency is not better understood, detailed information on future tree growth can hardly be provided.

6.2 Forest Management Decisions with Uncertainty

Elaborating forest management related issues of modelled impacts determined following questions:

- What are the contributions of management and climate scenario effects on the uncertainty of future forest production in mixed oak-pine forest stands?
- Is it possible to apply a general evaluation criteria from literature on a specific forest stand which is representative for the forest transformation in Brandenburg?

The methodological framework to investigate combined effects of management and climate scenarios on a specific forest stand allows an integrated assessment of management strategies under changing climate conditions. The usage of the total performance index helps forest authorities to include the huge variety of future climate scenarios and, thus to formalize the decision making process.

The analysis of variance of growth related model outputs and the CDFs of the TPI showed an increase of climate uncertainty with increasing climate warming. Interestingly, the increase of climate induced variation is much higher from 2 to 3 K than from 0 to 2 K and outrun the forest management induced variation at 3 K. This exemplifies the non-linear impacts of climate change on forest growth.

Although the variance in the modelled growth of pine and oak trees is increased, my thesis does not discover general concerns about the ability of oak-pine forests under climate change. In average the potential net primary production of oak and pine is increasing, except for only few realisations of the 3 K scenario. However, for the total assessment of the ability of trees to adapt to changing climate conditions also biotic factors (i.e. insect calamities, pathogens) have to be taken into account. There are strong hints of decreasing carbon sink capacity in the European forest also due to increased calamities (Nabuurs et al., 2013). The future generation of forest related climate impact models has to consider changing biotic influences on

forest productivity (Klein et al., 2013).

Chapter 7

Conclusion and Outlook

The chapter three focused on tree specific productivity at the regional level. Hereby, the productivity in terms of net primary production (NPP) has been evaluated using regression functions which originate from a model reduction framework.

Those functions, which calculate an average annual NPP from mean climate and soil parameters, enable plausible biomass predictions with easily accessible environmental data. I used the functions for an efficient classification of climate impacts on tree species considering regional specific productivity and multiple climate scenarios. The functions are also suitable to improve climate insensitive forest growth models which would enhance the forest model applicability.

Overall, I found a positive trend of tree and stand productivity (*spruce* less *beech* less *oak* less *pine*) for almost all regions in Germany until 2060. The lowest positive changes combined with highest climate scenario uncertainty can be found in the north-eastern German lowlands. The higher the elevation of a forest eco-region, the higher will be the relative increase of the NPP due to limitations by temperature in the mountainous regions.

In chapter four I compared two different root water uptake approaches with respect to tree growth, soil water and transpiration. The more complex and process-based approach better captured the real non-linear behaviour of the root water uptake. This is shown by the improved drought sensitivity of the approach, when compared to *in situ* tree ring measurements. However, taking into account all validation levels no approach could be identified as the "best" approach.

In comparison to the empirical approach the higher parameter demand of the process-based approach limits its applicability, especially on multi-forest stand applications (e.g. chapter three). On the small scale (single stand modelling studies), the process-based approach shall be preferred.

In chapter five, the application of a framework considering climate scenario and forest management uncertainty in order to evaluate forest management strategies was tested at a mixed oak-pine stand. It is shown quantitatively how climate change and forest management impacts affect forest stand productivity. The work revealed a strong increase of climate change effects on stand productivity at a temperature increase higher than 2 K. The tested multi-objective assessment approach proved to be useful for forest management planning under climate scenario uncertainty. It has the potential to support the development of adaptation strategies for time periods longer than 50 years for the ongoing forest transformation.

Bibliography

- Alcamo, J., Moreno, J., Novky, B., Bindi, M., Corobov, R., Devoy, R., Giannakopoulos, C., Martin, E., Olesen, J., and Shvidenko, A. (2007). Europe. climate change 2007: Impacts, adaptation and vulnerability. contribution of working group ii to the fourth assessment report of the intergovernmental panel on climate change. Technical report, Intergovernmental Panel on Climate Change, Cambridge.
- Ammer, C. and Wagner, S. (2005). An approach for modelling the mean fine-root biomass of norway spruce stands. *Trees - Structure and Function*, 19:145–153.
- Ananda, J. and Herath, G. (2009). A critical review of multi-criteria decision making methods with special reference to forest management and planning. *Ecological Economics*, 68(10):2535 – 2548.
- Anders, S., Beck, W., Hornschuch, F., Müller, J., and Steiner, A. (2005). Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes - ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. In *Ökologischer Waldumbau im nordostdeutschen Tiefland*, pages 12–32. LFE (Landeskompetenzzentrum Forst Eberswalde).
- Arneth, A., Lloyd, J., Santruckova, H., Bird, M., Grigoryev, S., Kalaschnikov, Y.,

- Gleixner, G., and Schulze, E. (2002). Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO_2 concentration. *Global Biogeochemical Cycles*, 16(1):5–1–5–13.
- Beck, W. (2007). Analyse des Wachstumsverhaltens von Kiefern-Beständen auf unterschiedlichen zeitlichen Skalenebenen. pages 341–357. Eberswalder Forstliche Schriftenreihe XXXII, Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz (MLUV) des Landes Brandenburg.
- Beck, W. (2009). Growth patterns of forest stands-the response towards pollutants and climatic impact. *iForest*, 2:4–6.
- Beniston, M. (2010). Weather and climate extremes: Where can dendrochronology help? In Stoffel, M., Bollschweiler, M., Butler, R. D., and Luckman, H. B., editors, *Tree Rings and Natural Hazards: A State-of-Art*, pages 283–290. Springer Netherlands, Dordrecht.
- BGR (1998). Bodenübersichtskarte der Bundesrepublik Deutschland 1:100.000.000 (BÜK 1000). Technical report, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover.
- Bittner, S., Talkner, U., Kramer, I., Beese, F., Holscher, D., and Priesack, E. (2010). Modeling stand water budgets of mixed temperate broad-leaved forest stands by considering variations in species specific drought response. *Agricultural And Forest Meteorology*, 150(10):1347–1357.
- BMELF (1994). Nationaler Waldbericht. Technical report, Bundesministerium für Ernährung, Landwirtschaft und Forsten.

- BMUNR (2008). Deutsche Anpassungsstrategie an den Klimawandel. (vom Bundeskabinett am 17. Dezember 2008 beschlossen). Technical report, Bundeskabinett.
- Boisvenue, C. and Running, S. W. (2006). Impacts of climate change on natural forest productivity: evidence since the middle of the 20th century. *Global Change Biology*, 12:1–21.
- Bolte, A., Ammer, C., Lf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P., and Rock, J. (2009). Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scandinavian Journal Of Forest Research*, 24:473–482.
- Borchers, J. (2010). Segregation versus Multifunktionalität in der Forstwirtschaft. *AFZ / Der Wald*, 65(7/8):44–48.
- Breda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals Of Forest Science*, 63(6):625–644.
- Broadmeadow, M. and Jackson, S. (2000). Growth responses of *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* to elevated carbon dioxide, ozone and water supply. *New Phytologist*, 146(3):437–451.
- Bugmann, H., Grote, R., Lasch, P., Lindner, M., and Suckow, F. (1997). A new forest gap model to study the effects of environmental change on forest structure and functioning. In Mohren, G. M. J., Kramer, K., and Sabaté, S., editors, *Impacts of Global Change of Tree Physiology and Forest Ecosystem*, pages 255–261. Kluwer Academic Publisher, Dordrecht.

- Bundestag (2004). Gesetz für den Vorrang erneuerbarer Energien. Technical report, Bundestag, Deutscher.
- Campbell, G. S. (1991). Simulations of water uptake by plant roots. In Hanks, J. and Ritchie, J., editors, *Modeling plant and soil systems*, pages 273–285. American Society of Agronomy, Madison, Wisconsin, USA.
- CEC (2007). Renewable energy road map renewable energies in the 21st century: building a more sustainable future. Technical report, Brussels, Belgium.
- Centritto, M., Lucas, M., and Jarvis, P. (2002). Gas exchange, biomass, whole-plant water-use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. *Tree Physiology*, 22(10):699–706.
- Chen, C. W. (1993). The response of plants to interacting stresses: PGSM Version 1.3 Model Documentation. Technical Report TR-101880, Electric Power Res. Inst., Palo Alto, USA.
- Chermack, T. J. (2004). A theoretical model of scenario planning. *Human Resource Development Review*, 3(4):301–325.
- Chermack, T. J., Lynham, S. A., and Ruona, W. E. A. (2001). A review of scenario planning literature. *Futures Research Quarterly*, 17(2):7–31.
- Chuang, Y., Oren, R., Bertozzi, A., Phillips, N., and Katul, G. (2006). The porous media model for the hydraulic system of a conifer tree: Linking sap flux data to transpiration rate. *Ecological Modelling*, 191(3-4):447–468.

- Ciais, P., Schelhaas, M. J., Zaehle, S., Piao, S. L., Cescatti, A., Liski, J., Luysaert, S., Le-Maire, G., Schulze, E. D., Bouriaud, O., Freibauer, A., Valentini, R., and Nabuurs, G. J. (2008). Carbon accumulation in european forests. *Nature Geoscience*, 1(7):425–429.
- Coners, H. (2001). *Wasseraufnahme und artspezifische hydraulische Eigenschaften der Feinwurzeln von Buche, Eiche und Fichte: In situ-Messungen an Altbäumen*. PhD thesis, Georg-August-Universität Göttingen, Mathematisch-Naturwissenschaftliche Fakultäten der Georg-August-Universität zu Göttingen, Göttingen.
- Coners, H. and Leuschner, C. (2005). In situ measurement of fine root water absorption in three temperate tree species - temporal variability and control by soil and atmospheric factors. *Basic And Applied Ecology*, 6(4):395–405.
- Cowan, I. R. (1965). Transport of water in the soil-plant-atmosphere system. *Journal of Applied Ecology*, 2(1):221–239.
- Cruziat, P., Cochard, H., and Ameglio, T. (2002). Hydraulic architecture of trees: main concepts and results. *Annals Of Forest Science*, 59(7):723–752.
- Davidson, R. L. (1969). Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Annals of Botany*, 33(3):561–569.
- Dillaway, D. N. and Kruger, E. L. (2010). Thermal acclimation of photosynthesis: a comparison of boreal and temperate tree species along a latitudinal transect. *Plant, Cell & Environment*, 33(6):888–899.

- Doussan, C., Pages, L., and Vercambre, G. (1998). Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption - model description. *Annals Of Botany*, 81(2):213–223.
- Dreyer, E., Le Roux, X., Montpied, P., Daudet, F. A., and Masson, F. (2001). Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiology*, 21(4):223–232.
- Duquesnay, A., Breda, N., Stievenard, M., and Dupouey, J. (1998). Changes of tree-ring delta C-13 and water-use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant Cell and Environment*, 21(6):565–572.
- DVWK (1996). *Ermittlung der Verdunstung von Land- und Wasserflächen*. Wirtschafts- und Verlagsgesellschaft Gas und Wasser mbH Bonn, Bonn.
- DWD (2012). Zahlen und Fakten zum Klimawandel in Deutschland. In *Klima-Presskonferenz*.
- Elmer, M., Bachmann, U., Gutsch, M., Schröder, J., Bäucker, E., Lange, M., Clauser, L., Bens, O., Suckow, F., Kätzel, R., Bues, C.-T., Frommhold, H., Sonntag, H., Fischer, T., and Hüttl, R. F. (2009a). OakChain: Eichen-Kiefern-Mischbestände im Spannungsfeld von Klimawandel, Waldumbau und internationalem Holzmarkt. *Forst und Holz*, 64(7/8):26–29.
- Elmer, M., Gutsch, M., Bachmann, U., Bens, O., Suckow, F., and Hüttl, F. (2009b). Der Einfluss des Umbaus von Kiefern-Reinbeständen in Traubeneichen-Kiefern-Mischwälder auf Standortqualität und Bestandesklima. *Forst und Holz*, 64(3):12–17.

- Elmer, M., Kätzel, R., Bens, O., Bues, C.-T., Sonntag, H., and Hüttl, R. (2009c). *Nachhaltige Bewirtschaftung von Eichen-Mischbeständen*. Oekom Verlag, München.
- Endtmann, K.-J. (2007). Taxonomie, artmerkmale und verbreitung der gewöhnlichen kiefer. In *Die Kiefer im nordostdeutschen Tiefland - Ökologie und Bewirtschaftung*, Eberswalder Forstliche Schriftenreihe Band 32. Landeskompetenzzentrum Eberswalde.
- EUFORGEN (2009). Distribution map of scots pine (pinus sylvestris).
- Farquhar, G. D. and Sharkey, T. D. (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, 33:317–345.
- Feng, X. (1999). Trends in intrinsic water-use efficiency of natural trees for the past 100-200 years: A response to atmospheric CO_2 concentration. *Geochimica et Cosmochimica Acta*, 63(13-14):1891–1903.
- Fontes, L., Bontemps, J. D., Bugmann, H., Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., , and Skovsgaard, J. P. (2010). Models for supporting forest management in a changing environment. *Forest Research*, 19:8–29.
- Friedrichs, D. A., Buentgen, U., Frank, D. C., Esper, J., Neuwirth, B., and Loeffler, J. (2009). Complex climate controls on 20th century oak growth in Central-West Germany. *Tree Physiology*, 29(1):39–51.
- Fürstenau, C. (2008). *The impact of silvicultural strategies and climate change on carbon sequestration and other forest ecosystem functions*. PhD thesis, Universität Potsdam, Institut für Geoökologie, Potsdam.

- Galiano, L., Martnez-Vilalta, J., and Lloret, F. (2010). Drought-induced multifactor decline of scots pine in the pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 13(7):978–991.
- Gerten, D., Luo, Y., Le Maire, G., Parton, W. J., Keough, C., Weng, E., Beier, C., Ciais, P., Cramer, W., Dukes, J. S., Hanson, P. J., Knapp, A. A. K., Linder, S., Nepstad, D., Rustad, L., and Sowerby, A. (2008). Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, 14(10):2365–2379.
- Gieger, T. (2002). *Effects of Drought and Defoliation on Water Relations of Pedunculate and Sessile Oak*. PhD thesis, Georg-August-Universität Göttingen.
- Gimmi, U., Wohlgemuth, T., Rigling, A., Hoffmann, C., and Bürgi, M. (2010). Land-use and climate change effects in forest compositional trajectories in a dry central-alpine valley. *Annals of Forest Science*, 67:701–701.
- Glugla, G. (1969). Berechnungsverfahren zur Ermittlung des aktuellen Wassergehaltes und Gravitationswasserabflusses im Boden. *Albrecht-Thaer-Archiv*, 13:371–376.
- Granier, A. and Loustau, D. (1994). Measuring and modeling the - transpiration of a maritime pine canopy from sap-flow data. *Agricultural And Forest Meteorology*, 71(1-2):61–81.
- Granier, A., Reichstein, M., Breda, N., Janssens, I. A., Falge, E., Ciais, P., Gruenwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Koestner, B.,

Bibliography

- Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, I., and Wang, Q. (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(1-2):123–145.
- Grant, R. F., Arain, A., Arora, V., Barr, A., Black, T. A., Chen, J., Wang, S., Yuan, F., and Zhang, Y. (2005). Intercomparison of techniques to model high temperature effects on CO_2 and energy exchange in temperate and boreal coniferous forests. *Ecological Modelling*, 188(2-4):217–252.
- Grote, R. and Suckow, F. (1998). Integrating dynamic morphological properties into forest growth modeling. i. effects on water balance and gas exchange. *Forest Ecology and Management*, 112:101–119.
- Hacke, U. G., Sperry, J. S., Ewers, B. E., Ellsworth, D. S., Schäfer, K. V. R., and Oren, R. (2000). Influence of soil porosity on water use in pinus taeda. *Oecologia*, 124:495–505.
- Hanson, P. J., Amthor, J. S., Wullschleger, S. D., Wilson, K. B., Grant, R. F., Hartley, A., Hui, D., Hunt, J. E. R., Johnson, D. W., Kimball, J. S., King, A. W., Luo, Y., McNulty, S. G., Sun, G., Thornton, P. E., Wang, S., Williams, M., Baldocchi, D. D., and Cushman, R. M. (2004). Oak forest carbon and water simulations: Model intercomparisons and evaluations against independent data. *Ecological Monographs*, 74:443–489.
- Haxeltine, A. and Prentice, I. C. (1996). Biome3: An equilibrium terrestrial bio-

- sphere model based on ecophysiological constraints, resource availability and competition among plant functional types. *Global Biogeochemical Cycles*, 10(4):693–709.
- Helama, S., Laanelaid, A., Raisio, J., and Tuomenvirta, H. (2009). Oak decline in Helsinki portrayed by tree-rings, climate and soil data. *Plant and Soil*, 319(1-2):163–174.
- Henschel, A. (2008). Habitatmodellierung der drei Baumarten Waldkiefer, Traubeneiche und Stieleiche. Master’s thesis, Humboldt-Universität zu Berlin.
- Hofmann, G. and Pommer, U. (2005). *Potentielle Natürliche Vegetation von Brandenburg und Berlin*. Eberswalder Forstliche Schriftenreihe Band 24. Bäßler Verlag.
- Holst, J., Grote, R., Offermann, C., Ferrio, J., Gessler, A., Mayer, H., and Rennenberg, H. (2010). Water fluxes within beech stands in complex terrain. *International Journal of Biometeorology*, 54(1):23–36.
- Holsten, A., Vetter, T., Vohland, K., and Krysanova, V. (2009). Impact of climate change on soil moisture dynamics in brandenburg with a focus on nature conservation areas. *Ecological Modelling*, 220(17):2076 – 2087.
- Hornschuch, F., Krakau, U., and Riek, W. (2007). Das Wurzelsystem der Kiefer - artspezifische Strategie und ökologische Anpassungen. In *Die Kiefer im nordostdeutschen Tiefland - Ökologie und Bewirtschaftung*, Eberswalder Forstliche Schriftenreihe Band XXXII. LFE (Landeskompetenzzentrum Forst Eberswalde).
- Hunt, E. R., Running, S. W., and Federer, C. A. (1991). Extrapolating plant

Bibliography

- water flow resistances and capacitances to regional scales. *Agricultural and Forest Meteorology*, 54(24):169 – 195.
- Ibanez, I., Clark, J. S., Dietze, M. C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N. E., and Wolosin, M. S. (2006). Predicting biodiversity change: Outside the climate envelope, beyond the species-area curve. *Ecology*, 87(8):1896–1906.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108(3):389–411.
- Jacobsen, J. and Thorsen, B. (2003). A Danish example of optimal thinning strategies in mixed-species forest under changing growth conditions caused by climate change. *Forest Ecology and Management*, 180(1-3):375–388.
- Jansson, P.-E. (1998). *Simulating Model for Soil Water and Heat Conditions. Description of the SOIL model*. Swedish University of Agricultural Sciences Department of Soil Sciences Division of Agricultural Hydrotechnics.
- Jarvis, A. J. and Davies, W. J. (1998). The coupled response of stomatal conductance to photosynthesis and transpiration. *Journal of Experimental Botany*, 49(special issue):399–406.
- Jenssen, M. (2009). Der klimaplastische Wald im nordostdeutschen Tiefland-Strategie der forstlichen Risikovorsorge angesichts einer unvorhersagbaren Zukunft. Technical report, Waldkunde-Institut Eberswalde GmbH.

- Jenssen, M., Weber, D., Konnert, M., Hosius, B., Schaefer, M., Jansen, M., Rothenbuecher, J., Doering, C., Makeschin, F., Augustin, S., Anders, S., Mller, J., Rust, S., Papen, H., Brueggemann, N., Hanewinkel, M., Wilpert, K., U., H., and Selter, A. (2006). *Ökologischer Waldumbau in Deutschland*. oekom Verlag.
- Jochheim, H., Puhmann, M., Beese, F., Berthold, D., Einert, P., Kallweit, R., Konopatzky, A., Meesenburg, H., Meiwes, K. J., Raspe, S., Schulte-Bisping, H., and Schulz, C. (2009). Modelling the carbon budget of intensive forest monitoring sites in germany using the simulation model biome-bgc. *iForest - Biogeosciences and Forestry*, 2(1):7–10.
- Johnsen, K., Samuelson, L., Teskey, R., Mcnulty, S., and Fox, T. (2001). Process Models as Tools in Forestry Research and Management. *Forest Science*, 47(1):2–8.
- Jung, T., Blaschke, H., and Osswald, W. (2000). Involvement of soilborne phytophthora species in central european oak decline and the effect of site factors on the disease. *Plant Pathology*, 49(6):706–718.
- Kätzel, R., Löffler, S., and Wenk, M. (2006). Physiologische Reaktionen von Eichen unter Trockenstress. In *Aktuelle Ergebnisse und Fragen zur Situation der Eiche und ihrer Bewirtschaftung in Brandenburg*. LFE (Landeskompetenzzentrum Forst Eberswalde).
- Keenan, T., García, R., Friend, A. D., Zaehle, S., Gracia, C., and Sabate, S. (2009). Improved understanding of drought controls on seasonal variation in Mediterranean forest canopy CO_2 and water fluxes through combined in situ measurements and ecosystem modelling. *Biogeosciences*, 6(8):1423–1444.

- Keenan, T., Sabate, S., and Gracia, C. (2010). Soil water stress and coupled photosynthesis-conductance models: Bridging the gap between conflicting reports on the relative roles of stomatal, mesophyll conductance and biochemical limitations to photosynthesis. *Agricultural and Forest Meteorology*, 150(3):443–454.
- Kellomaki, S. and Wang, K. Y. (2000). Modelling and measuring transpiration from scots pine with increased temperature and carbon dioxide enrichment. *Annals Of Botany*, 85(2):263–278.
- Kirschbaum, M. U. F. (1999). CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling*, 118(1):17–59.
- Klein, D., Höllerl, S., Blaschke, M., and Schulz, C. (2013). The contribution of managed and unmanaged forests to climate change mitigation - a model approach at stand level for the main tree species in bavaria. *Forests*, 4(1):43–69.
- Koitzsch, R. (1977). Schätzung der Bodenfeuchte aus meteorologischen Daten, Boden- und Pflanzenparametern mit einem Mehrschichtmodell. *Zeitschrift für Meteorologie*, 27(5):302–306.
- Kölling, C. (2007). Klimahüllen für 27 Waldbaumarten. *AFZ / Der Wald*, 23:1242–1245.
- Kölling, C. and Ammer, C. (2006). Waldumbau unter den Vorzeichen des Klimawandels. *AFZ / Der Wald*, 20:1086–1089.
- Körner, C. (2006). Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist*, 172(3):393–411.

- Körner, C., Asshoff, R., Bignucolo, O., Hattenschwiler, S., Keel, S. G., Pelaez-Riedl, S., Pepin, S., Siegwolf, R. T. W., and Zotz, G. (2005). Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2 . *Science*, 309(5739):1360–1362.
- Kostner, B., Biron, P., Siegwolf, R., and Granier, A. (1996). Estimates of water vapor flux and canopy conductance of scots pine at the tree level utilizing different xylem sap flow methods. *Theoretical And Applied Climatology*, 53(1-3):105–113.
- Kozak, A. and Kozak, R. (2003). Does cross validation provide additional information in the evaluation of regression models? *Canadian Journal of Forest Research*, 33:976–987.
- Landsberg, J. (2003). Modelling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research*, 33(3):385–397.
- Landsberg, J. and Waring, R. (1997). A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, 95(3):209 – 228.
- Lang, A., Klepper, B., and Cumming, M. (1969). Leaf Water Balance During Oscillation of Stomatal Aperture. *Plant Physiology*, 44(6):826–830.
- Lasch, P., Badeck, F.-W., Lindner, M., and Suckow, F. (2002a). Sensitivity of simulated forest growth to changes in climate and atmospheric CO_2 . *Forstwissenschaftliches Centralblatt*, 121, Supplement 1:155–171.
- Lasch, P., Badeck, F. W., Suckow, F., Lindner, M., and Mohr, P. (2005). Model-

- based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *Forest Ecology And Management*, 207(1-2):59–74.
- Lasch, P., Gutsch, M., and Suckow, F. (2009a). Klimawandel in Brandenburg-Risiken für Eichen-Kiefern-Mischbestände. In *Wald im Klimawandel-Risiken und Anpassungsstrategien*, pages 14–21. LFE (Landeskompetenzzentrum Forst Eberswalde).
- Lasch, P., Lindner, M., Erhard, M., Suckow, F., and Wenzel, A. (2002b). Regional impact assessment on forest structure and functions under climate change - the brandenburg case study. *Forest Ecology and Management*, 162(1):73–86.
- Lasch, P., Schröder, J., Suckow, F., Gutsch, M., and Degenhardt, A. (2009b). Nutzung von Modellen zur Vorbereitung auf die Zukunft. In Elmer, M., Kätzel, R., Bens, O., Bues, C.-T., Sonntag, H., and Hüttl, R. F., editors, *Nachhaltige Bewirtschaftung von Eichen-Mischbeständen*, pages 119–135. Oekom Verlag, München.
- Lehtonen, A., Makipaa, R., Heikkinen, J., Sievanen, R., and Liski, J. (2004). Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. *Forest Ecology And Management*, 188(1-3):211–224.
- Lenoir, J., Ggout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884):1768–1771.
- Lindner, M. (2000). Developing adaptive forest management strategies to cope with climate change. *Tree Physiology*, 20(5-6):299–307.

- Lindner, M. and Cramer, W. (2002). German forest sector under global change: An interdisciplinary impact assessment. *Forstwissenschaftliches Centralblatt*, 121:3–17.
- Lindner, M., Garcia-Gonzalo, J., Kolström, M., Green, T., Reguera, R., Maroschek, M., Seidl, R., Lexer, M., Netherer, S., Schopf, A., Kremer, A., Delzon, S., Barbati, A., Marchetti, M., and Corona, P. (2008). Impacts of climate change on european forests and options for adaptation. Technical report, European Forest Institute (EFI), Joensuu.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolstrom, M., Lexer, M. J., and Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of european forest ecosystems. *Forest Ecology And Management*, 259(4):698–709.
- Loehle, C. and LeBlanc, D. (1996). Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling*, 90(1):1 – 31.
- Lozán, J. L. and Kausch, H. (2007). *Angewandte Statistik für Naturwissenschaftler*. Parey, Hamburg.
- Lundblad, M. and Lindroth, A. (2002). Stand transpiration and sapflow density in relation to weather, soil moisture and stand characteristics. *Basic And Applied Ecology*, 3(3):229–243.
- Luthardt, M. E. (2005). Waldbauliche Schlussbetrachtungen. In *Ökologischer Waldumbau im nordostdeutschen Tiefland*. LFE (Landeskompetenzzentrum Forst Eberswalde).

- Luthardt, M. E. (2006). *Bestandeszieltypen für die Wälder des Landes Brandenburg*. MLUV.
- Lüttschwager, D., Rust, S., Wulf, M., Forkert, J., and Hüttl, R. F. (1999). Tree canopy and herb layer transpiration in three scots pine stands with different stand structure. *Annals Of Forest Science*, 56(4):265–274.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., GrNwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyrá, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M. L., Tang, J., Valentini, R., Vesala, T., and Janssens, I. A. (2007). CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, 13(12):2509–2537.
- Maherali, H., Moura, C., Caldeira, M., Willson, C., and Jackson, R. (2006). Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant Cell and Environment*, 29(4):571–583.
- Mäkelä, A., Landsberg, J., Ek, A., Burk, T., Ter-Mikaelian, M., Agren, G., Oliver, C., and Puttonen, P. (2000). Process-based models for forest ecosystem manage-

Bibliography

- ment: current state of the art and challenges for practical implementations. *Tree Physiology*, 20:289–298.
- Maroschek, M., Seidl, R., and Lexer, M. J. (2009). Climate change impacts on goods and services of european mountain forests. *Unasylva*, 60(231/232):76–80.
- Matias, L. and Jump, A. S. (2012). Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of *pinus sylvestris*. *Forest Ecology and Management*, 282(0):10 – 22.
- McGill, R., Tukey, J. W., and Larsen, W. A. (1978). Variations of box plots. *The American statistician*, 32(1):12–16.
- McKenney, M. S. and Rosenberg, N. J. (1993). Sensitivity of some potential evapotranspiration estimation methods to climate change. *Agricultural and Forest Meteorology*, 64(12):81 – 110.
- Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A., and Jarvis, P. G. (2002). Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. *Plant, Cell & Environment*, 25(3):343–357.
- Menzel, A., Estrella, N., and Fabian, P. (2001). Spatial and temporal variability of the phenological seasons in germany from 1951 to 1996. *Global Change Biology*, 7(6):657–666.
- Menzel, A., Estrella, N., Heitland, W., Susnik, A., Schleip, C., and Dose, V. (2008). Bayesian analysis of the species-specific lengthening of the growing season in two

Bibliography

- European countries and the influence of an insect pest. *International Journal of Biometeorology*, 52(3):209–218.
- MIL (2011). Waldzustandsbericht 2011 der Länder Brandenburg und Berlin. Technical report, Ministerium für Infrastruktur und Landwirtschaft des Landes Brandenburg.
- Möller, K., Walter, C., Engelmann, A., and Hielscher, K. (2007). Die Gefährdung der Gemeinen Kiefer durch Insekten. In *Die Kiefer im nordostdeutschen Tiefland - Ökologie und Bewirtschaftung*, Eberswalder Forstliche Schriftenreihe Band 32. Landeskompetenzzentrum Eberswalde.
- Monteith, J. L. (1995). Accomodation between transpiring vegetation and the convective boundary layer. *Journal of Hydrology*, 166:251–263.
- Müller, J. and Luthardt, M. E. (2009). Wald- und Kiefernland Brandenburg. *AFZ / Der Wald*, 64:2–4.
- Murphy, J. (2000). Predictions of climate change over Europe using statistical and dynamical downscaling techniques. *International Journal of Climatology*, 20(5):489–501.
- Nabuurs, G.-J., Lindner, M., Verkerk, P. J., Gunia, K., Deda, P., Michalak, R., and Grassi, G. (2013). First signs of carbon sink saturation in European forest biomass. *Nature Climate Change*, 3:792–796.
- Nakicenovic, N., Alcamo, J., Davis, G., Vries, B. D., Fenhann, J., Gaffin, S., Gregory, K., Griibler, A., Jung, T. Y., Kram, T., Lebre, E., Rovere, L., Michaelis, L., Mori,

Bibliography

- S., Morita, T., Smith, S., Swart, R., Rooijen, S. V., Victor, N., and Dadi, Z. (2000). *Emissions scenarios*. Cambridge University Press, Cambridge.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myneni, R. B., and Running, S. W. (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300(5625):1560–1563.
- Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R. (2005). Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 102(50):18052–18056.
- Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, 107(45):19368–19373.
- Norby, R. J. and Zak, D. R. (2011). Ecological Lessons from Free-Air CO_2 Enrichment (FACE) Experiments. In Futuyma, DJ and Shaffer, HB and Simberloff, D, editor, *Annual Review of Ecology, Evolution, and Systematics*, volume 42, pages 181–203.
- Oene, H. v., Berendse, F., Persson, T., Harrison, T., Schulze, E.-D., Andersen, B., G.A.Bauer, Dambrine, E., Högberg, P., Matteucci, G., and Paces, T. (2000).

- Model analysis of carbon and nitrogen cycling in picea and fagus forests. In Schulze, E.-D., editor, *Carbon and Nitrogen Cycling in European Forest Ecosystems*, pages 419–467. Springer, Berlin.
- Orlowsky, B., Gerstengarbe, F. W., and Werner, P. C. (2008). A resampling scheme for regional climate simulations and its performance compared to a dynamical rcm. *Theoretical And Applied Climatology*, 92(3-4):209–223.
- Österle, H., Gerstengarbe, F.-W., and Werner, P. C. (2006). Ein neuer meteorologischer Datensatz für Deutschland, 1951 - 2003. In *7. Deutsche Klimatagung - Klimatrends: Vergangenheit und Zukunft.*, page 3, München. Meteorologisches Institut der Ludwig-Maximilians-Universität.
- Ostonen, I., Lohmus, K., Helmisaari, H. S., Truu, J., and Meel, S. (2007). Fine root morphological adaptations in scots pine, norway spruce and silver birch along a latitudinal gradient in boreal forests. *Tree Physiology*, 27(11):1627–1634.
- Panferov, O., Doering, C., Rauch, E., Sogachev, A., and Ahrends, B. (2009). Feedbacks of windthrow for norway spruce and scots pine stands under changing climate. *Environmental Research Letters*, 4(4):045019.
- Parry, M., Canziani, O., Palutikof, J., van der Linden, P., and Hanson, C. (2007). *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007*. Cambridge University Press.
- Peel, M. C., Finlayson, B. L., and McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and earth system sciences*, 11(5):1633–1644.

- Piao, S. L., Friedlingstein, P., Ciais, P., Peylin, P., Zhu, B., and Reichstein, M. (2009). Footprint of temperature changes in the temperate and boreal forest carbon balance. *Geophysical Research Letters*, 36:1–5.
- PIK (2012). Characterization of STAR 2.0 regional climate scenarios with 0.5 K temperature increase. (unpublished).
- Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., and Maugeri, M. (2008). Drought-driven growth reduction in old beech (*fagus sylvatica* l.) forests of the central apennines, italy. *Global Change Biology*, 14(6):1265–1281.
- Poyatos, R., Martnez-Vilalta, J., Cermk, J., Ceulemans, R., Granier, A., Irvine, J., Köstner, B., Lagergren, F., Meiresonne, L., Nadezhdina, N., Zimmermann, R., Llorens, P., and Mencuccini, M. (2007). Plasticity in hydraulic architecture of scots pine across eurasia. *Oecologia*, 153(2):245–259.
- Prato, T. (2008a). Accounting for risk and uncertainty in determining preferred strategies for adapting to future climate change. *Mitigation and Adaptation Strategies for Global Change*, 13(1):47–60.
- Prato, T. (2008b). Conceptual framework for assessment and management of ecosystem impacts of climate change. *Ecological Complexity*, 5(4):329–338.
- Pretzsch, H. (2009). *Forest Dynamics, Growth and Yield: From Measurement to Model.*, chapter From primary production to growth and harvestable yield and vice versa: specific definitions and the link between two branches of forest science., pages 41–99. Springer-Verlag Berlin Heidelberg.

- Pucko, C., Beckage, B., Perkins, T., and Keeton, W. S. (2011). Species shifts in response to climate change: Individual or shared responses? *Journal of the Torrey Botanical Society*, 138(2):156–176.
- Pussinen, A., Nabuurs, G. J., Wieggers, H. J. J., Reinds, G. J., Wamelink, G. W. W., Kros, J., Mol-Dijkstra, J. P., and de Vries, W. (2009). Modelling long-term impacts of environmental change on mid- and high-latitude european forests and options for adaptive forest management. *Forest Ecology And Management*, 258(8):1806–1813.
- R Development Core Team (2009). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raisanen, J., Hansson, U., Ullerstig, A., Doscher, R., Graham, L., Jones, C., Meier, H., Samuelsson, P., and Willen, U. (2004). European climate in the late twenty-first century: regional simulations with two driving global models and two forcing scenarios. *Climate Dynamics*, 22(1):13–31.
- Rebetez, M. and Dobbertin, M. (2004). Climate change may already threaten scots pine stands in the swiss alps. *Theoretical and Applied Climatology*, 79(1):1–9.
- Reich, P. B. and Oleksyn, J. (2008). Climate warming will reduce growth and survival of scots pine except in the far north. *Ecology Letters*, 11:588–597.
- Reyer, C., Bachinger, J., Bloch, R., Hattermann, F., Ibisch, P., Kreft, S., Lasch, P., Lucht, W., Nowicki, C., Spathelf, P., Stock, M., and Welp, M. (2012). Climate change adaptation and sustainable regional development: a case study for the Federal State of Brandenburg, Germany. *Regional Environmental Change*, 12(3):523–542.

- Riek, W. and Stähr, F. (2004). *Eigenschaften typischer Waldböden im Nordost-deutschen Tiefland unter besonderer Berücksichtigung des Landes Brandenburg*. Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Eberwalder Forstliche Schriftenreihe XIX, Eberswalde.
- Ritchie, J. T. (1972). Model for predicting evaporation from a row crop with incomplete cover. *Water Resour. Res.*, 8(5):1204–1213.
- Ruosteenoja, K., Tuomenvirta, H., and Jylh, K. (2006). GCM-based regional temperature and precipitation change estimates for Europe under four SRES scenarios applying a super-ensemble pattern-scaling method. Technical report, Finnish Meteorological Institute.
- Saltelli, A., Tarantola, S., and Chan, K. (1999). A quantitative model-independent method for global sensitivity analysis of model output. *Technometrics*, 41(1):39–56.
- Sang, W. G. and Su, H. X. (2009). Interannual NPP variation and trend of *Picea schrenkiana* forests under changing climate conditions in the Tianshan Mountains, Xinjiang, China. *Ecological Research*, 24(2):441–452.
- Savolainen, O., Kujala, S. T., Sokol, C., Pyhajarvi, T., Avia, K., Knurr, T., Karkkainen, K., and Hicks, S. (2011). Adaptive Potential of Northernmost Tree Populations to Climate Change, with Emphasis on Scots Pine (*Pinus sylvestris* L.). *Journal of Heredity*, 102(5):526–536.
- Scarascia-Mugnozza, G., Bauer, G. A., Persson, H., Matteucci, G., and Masci, A. (2000). Tree biomass, growth and nutrient pools. In Schulze, E.-D., editor, *Carbon*

- and Nitrogen Cycling in European Forest Ecosystems*, pages 49–62. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Schaber, J. and Badeck, F.-W. (2003). Physiology based phenology models for forest tree species in germany. *International Journal of Biometeorology*, 47(7):193–201.
- Schmid, F. and Trede, M. (2006). *Finanzmarktstatistik*. Springer, Heidelberg.
- Schröder, J., Löffler, S., Michel, A., and Kätzel, R. (2009). Genetische Differenzierung, Zuwachsentwicklung und Witterungseinfluß in Mischbeständen von Traubeneiche und Kiefer. *Forst und Holz*, 64(3):18–24.
- Seidl, R., Rammer, W., and Lexer, M. (2011). Climate change vulnerability of sustainable forest management in the eastern alps. *Climatic Change*, 106(2):225–254.
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. (1964). A quantitative analysis of plant form - the pipe model theory i. basic analyses. *Japanese Journal of Ecology*, 14(3):97–105.
- Sinoquet, H., Le Roux, X., Adam, B., Ameglio, T., and Daudet, F. A. (2001). Ratp: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant, Cell & Environment*, 24(4):395–406.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C., and Woodward, F. I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography

Bibliography

- and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14(9):2015–2039.
- Skovsgaard, J. P., Stupak, I., and 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. *Scandinavian Journal of Forest Research*, 21(6):470–488.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M., and Miller, H. (2007). *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007*. Cambridge University Press.
- Spathelf, P., Bilke, G., Bolte, A., Foos, E., Hoepfner, K., Ibsch, P. L., Ktzel, R., Luthardt, M. E., Nusko, N., and Steinhardt, U. (2008). Eberswalder Erklärung. *AFZ / Der Wald*, 23:1254–1255.
- Spiecker, H. (2001). Tree rings and forest management in Europe. *Dendrochronologia*, 20(1-2):191–202.
- Thomas, F. M., Blank, R., and Hartmann, G. (2002). Abiotic and biotic factors and their interactions as causes of oak decline in central europe. *Forest Pathology*, 32(4-5):277–307.
- Thuiller, W., Lavorel, S., Arajo, M. B., Sykes, M. T., and Prentice, I. C. (2005). Climate change threats to plant diversity in europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102(23):8245–8250.

- UFZ (2010). *Nachhaltige Waldwirtschaft - Ein Förderschwerpunkt des Bundesministeriums für Bildung und Forschung in der Bilanz*. Helmholtz-Zentrum für Umweltforschung GmbH (UFZ).
- Vanclay, J. K. and Skovsgaard, J. P. (1997). Evaluating forest growth models. *Ecological Modelling*, 98(1):1–12.
- VanGenuchten, M. T. (1980). A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal*, 44(5):892–898.
- Walther, G.-R., Beiner, S., and Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16(5):541–548.
- Wang, Y., Bauerle, W. L., and Reynolds, R. F. (2008). Predicting the growth of deciduous tree species in response to water stress: FVS-BGC model parameterization, application, and evaluation. *Ecological Modelling*, 217(1-2):139–147.
- Waring, R. H. (1987). Characteristics of trees predisposed to die. *Bioscience*, 37(8):569–574.
- Wenk, M. and Apel, K.-H. (2007). Die Regenerationsfähigkeit von durch Fraß des Kiefernspinners (*Dendrolimus pini* L.) und der Nonne (*Lymantria monacha* L.) geschädigten Kiefernbeständen in Brandenburg. In *Die Kiefer im nordostdeutschen Tiefland - Ökologie und Bewirtschaftung*, Eberswalder Forstliche Schriftenreihe Band 32. Landeskompetenzzentrum Eberswalde.
- Wermelinger, B. (2004). Ecology and management of the spruce bark beetle *Ips ty-*

Bibliography

- pographus - a review of recent research. *Forest Ecology And Management*, 202:67–82.
- Williams, M., Bond, B. J., and Ryan, M. G. (2001a). Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. *Plant, Cell & Environment*, 24(7):679–690.
- Williams, M., Law, B. E., Anthoni, P. M., and Unsworth, M. H. (2001b). Use of a simulation model and ecosystem flux data to examine carbon-water interactions in ponderosa pine. *Tree Physiology*, 21(5):287–298.
- Williams, M., Rastetter, E. B., Fernandes, D. N., Goulden, M. L., Wofsy, S. C., Shaver, G. R., Melillo, J. M., Munger, J. W., Fan, S. M., and Nadelhoffer, K. J. (1996). Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell & Environment*, 19(8):911–927.
- Wilson, K. B., Hanson, P. J., Mulholland, P. J., Baldocchi, D. D., and Wullschleger, S. D. (2001). A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agricultural and Forest Meteorology*, 106(2):153–168.
- Wolff, B. (2002). Processing forest inventory data to establish a nationwide database for the estimation of the impacts of climate change on German forest and forestry. *Forstwissenschaftliches Centralblatt*, 121, Supplement 1:18–27.
- Wyka, T., Robakowski, P., and Zytkowskiak, R. (2007). Acclimation of leaves to contrasting irradiance in juvenile trees differing in shade tolerance. *Tree Physiology*, 27(9):1293–1306.

Bibliography

- Xiao, C. W., Janssens, I. A., Yuste, J. C., and Ceulemans, R. (2006). Variation of specific leaf area and upscaling to leaf area index in mature scots pine. *Trees-Structure And Function*, 20(3):304–310.
- Yousefpour, R., Jacobsen, J. B., Thorsen, B. J., Meilby, H., Hanewinkel, M., and Oehler, K. (2012). A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. *Annals of Forest Science*, 69(1):1–15.
- Zerbe, S. (2002). Restoration of natural broad-leaved woodland in central europe on sites with coniferous forest plantations. *Forest Ecology and Management*, 167:27–42.

Hiermit erkläre ich, dass die Arbeit an keiner anderen Hochschule eingereicht sowie selbstständig und nur mit den angegebenen Mitteln angefertigt wurde.

Potsdam, den 15.06.2015 (Martin Gutsch)