Projecting the carbon sink of managed forests based on standard forestry data

Ph.D. Dissertation

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For the deep love of my dear wife Christiane.

God's works are so great, worth
A lifetime of study—endless enjoyment!

(Psalm 111)

Table of contents

List of Publications

This thesis is based on the following Publications, which are referred to by their Roman numerals.

I. Wutzler, T., B. Köstner, and C. Bernhofer. 2006. Spatially explicit assessment of carbon stocks of a managed forest area in Eastern Germany. European Journal of Forest Research 126:371-381.

II. Wutzler, T., C. Wirth, and J. Schumacher. 2008. Generic biomass functions for Common beech (*Fagus sylvatica* L.) in Central Europe - predictions and components of uncertainty. Canadian Journal of Forest Research, 38 (6), June 2008.

III. Wutzler, T., and M. Mund. 2007. Modelling mean above and below ground litter production based on yield tables. Silva Fennica 41: 559-574.

IV. Wutzler, T., and M. Reichstein. 2007. Soils apart from equilibrium – consequences for soil carbon balance modelling. Biogeosciences 4:125-136.

V. Wutzler, T. 2008. Effect of the aggregation of multi-cohort mixed stands on modeling forest ecosystem carbon stocks. Silva Fennica submitted.

Statement about the own contribution to the Publications

Publication I

I performed the integration of the data sources, took and analyzed the soil samples, tested and implemented all the quantification and error propagation algorithms, planned and performed the statistical analysis. The coauthors helped with establishing contacts, acquiring the forestry data and several other administrative issues. They had supervised the work on the information system that was used in the Publication, contributed ideas about interpretation of the results, and helped with the formulation.

Publication II

Based upon a previous work of Christian Wirth for spruce, I designed and performed the statistical analysis for beech. My work on error propagation led to a different style of analysis (non-liner models) and to an extension of the statistical theory. Most of the original tree data was gathered by Christian Wirth. He also helped me with formulating my ideas and conclusion.

Publications III and IV

The entire study was performed by myself. The coauthors helped me with suggesting a few modifications of the analysis and with formulating my ideas and conclusion.

Publication V

The entire study was performed by myself. I thank Hannes Böttcher for a first internal review of the Publication before submission.

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Deutsche Zusammenfassung

Die Modellierung der Kohlenstoffdynamik in bewirtschafteten Forsten und deren Beeinflussung durch verschiedene Bewirtschaftungsoptionen ist das Anliegen dieser Doktorarbeit. Diese Modellierung wird benötigt um auch den Aspekt der Kohlenstoffspeicherung in Entscheidungen über verschiedene Bewirtschaftungsmaßnahmen zu berücksichtigen. Weiterhin ist die Modellierung ein viel versprechender Weg, um zwischen natürlichen und direkten anthropogenen Ursachen einer Kohlenstoffsenke oder Quelle zu unterscheiden, wie es von den Good Practicse Guidance Tier 3 vorgeschlagen ist (2003). In dieser Arbeit werden methodische Entwicklungen vorgestellt, mit der die Kohlenstoffdynamik in der Baumbiomasse, im Totholz, in der organischen Auflage, im Mineralboden und in Holzprodukten mit standardmäßig erhobenen Forstdaten simuliert werden kann.

Als beispielhaftes Untersuchungsgebiet wurden die Forsten des Bundeslandes Thüringen ausgewählt, da diese Region bereits in einigen Vorläuferprojekten zur Umsetzung des Kyotoprotokolls (Wirth et al. 2004, Mund et al. 2005) und zur Erfassung von Kohlenstoffvorräten (Baritz 2005) ausführlich untersucht wurde. Der größte Teil der 540.000 ha Forstfläche befindet sich auf den sauren Gesteinen des Thüringischen Schiefergebirges und des Thüringer Waldes und auf den Kalkstein-dominierten Flächen an den Rändern des Thüringer Beckens im Übergangsbereich vom maritimen zum kontinentalen Klima. Die dominierenden Baumarten der natürlichen Vegetation sind Fichte (*Picea abies*) in den höheren Lagen (500-980m), Buche (*Fagus sylvatica*) in den tieferen Lagen mit ausreichend Niederschlag, sowie Kiefer (*Pinus sylvestris*) und Eiche (*Quercus spec)* in den trockeneren Gebieten (Ozenda and Borel 2000). Teile der Flächen wurde vor allem im 13. Jahrhundert und einige Teile bis ins 20. Jahrhundert hinein landwirtschaftlich genutzt und auch ein Großteil der Böden der durchgängig als Wald genutzten Flächen wurde durch Waldweide und Streunutzung degradiert. Seit 1800 bevorzugte eine reguläre Forstwirtschaft vor allem Nadelhölzer, so dass ab der zweiten Hälfte des 20 Jahrhundert auf 70% der Fläche Nadelhölzer, vor allem Fichtenreinbestände wuchsen. Während sich die Forstwirtschaft früher vor allem an Ertragstafeln für Reinbestände orientierte, fördert sie heute gemischte mehrschichtige natürlichere Bestände.

Die Ergebnisse der Arbeit sind in dem Modell TreeGrOSS-C zusammengefasst, welches vier Teilmodelle koppelt: ein Bestandeswachstumsmodell, ein Bewirtschaftungsmodell, ein Modell der Kohlenstoffdynamik in Totholz, organischer Auflage und Boden und ein Modell der Kohlenstoffdynamik in Holzprodukten. Als Bestandeswachstumsmodell wurde das empirische Modell TreeGrOSS (Nagel 2003) ausgewählt, welches das Durchmesser- und Höhenwachstum von Einzelbäumen in gemischten Beständen simuliert. Es wurde um das Konzept von Kohorten, d.h. Gruppen ähnlicher Bäume, Forstinventurmodulen, und Modulen zur Berechnung von Kohlenstoff-Vorräten und Kohlenstoff-Umsätzen erweitert. Das erweiterte Modell wurde anhand von forstlichen Dauerversuchsflächen in Thürigen validiert. Als Ausgangspunkt für die Beschreibung der Kohlenstoffvorräte in Totholz, organischer Auflage und Mineralboden wurde das Modell YASSO (Liski et al. 2005) ausgewählt und so erweitert, dass es den Streueintrag gemischter Bestände simulieren konnte. Für die Beschreibung der Bewirtschaftung wurde ein ertragstafelbasiertes Modell entwickelt, und für die Holzprodukte wurde ein Modell entwickelt, welches auf Studien der Menge und der Lebensdauer von Holzprodukten in Thüringen beruht (Mund et al. 2005, Profft et al. 2007).

Die Berechnung aktueller Kohlenstoffvorräte im Forstökosystem war mit bereits etablierten Methoden möglich. Zusätzlich zu bisherigen Studien ermöglichte die Integration der forstlichen Grundkarte, der Standortkarte und Forstinventurdaten eine Untersuchung verschiedenster Einflussfaktoren auf die Kohlenstoffvorräte (Artikel I). Während die Durchforstungsintensität einen großen Einfluss hatte, wurde kein signifikanter Einfluss der Standortfaktoren im gleichen Klima auf die Kohlenstoffvorräte in der Baumbiomasse festgestellt.

Für die Fortschreibung der Kohlenstoffvorräte, also die Simulation der Kohlenstoffdynamik, war eine ergänzende Studie zu Biomassegleichungen für die Baumart Buche notwendig. In einer Meta-Analyse über die Originaldaten von 13 Studien wurde mit Hilfe gemischter Modelle ein Satz von Biomassegleichungen für alle wichtigen Biomassekompartimente entwickelt (Artikel II). Für die Baumart Buche existierten vorher nur Studien mit Originaldaten über einzelne Standorte oder Regionen, jedoch nicht für ganz Mitteleuropa. Auch in der Fehleranalyse ging die Studie über bisherige Arbeiten hinaus, indem sie erstmals den theoretischen statistischen Hintergrund für die Kovarianzen zwischen berechneten Einzelbaumbiomassen beschrieb, sowie Gleichungen und

Werkzeuge für die Berechnung der Kovarianzen und deren Hochskalierung in der Varianz der Biomasse auf Bestandesebene entwickelte. Sowohl die Vernachlässigung von Wuchsunterschieden zwischen Regionen, als auch die Vernachlässigung der Kovarianzen zwischen berechneten Einzelbaumbiomassen führt zu einer Unterschätzung der Varianz der Bestandesbiomassen.

Die größte methodische Herausforderung lag in der Initialisierung des Ausgangszustandes des Bodenmodells. Ähnliche bisherige Arbeiten hatten dazu die Annahme getroffen, dass sich die Bodenkohlenstoffvorräte im Gleichgewicht mit dem aktuellen Streueintrag befinden. Historisch bedingt, befinden sich die meisten Böden Mitteleuropas jedoch in einer Phase einer langsamen Erholung der Vorräte von früheren Störungen. Diese Arbeit geht in zwei Schritten über die strenge Gleichgewichtsannahme hinaus. Zum einen modellierte sie statt der aktuellen Streueinträge die durchschnittlichen Streueinträge über eine ganze Rotationsperiode eines Bestandes mit der Hauptbewirtschaftungsform des letzten Jahrhunderts (Artikel III). Diese Einträge umfassten zusätzlich zum Umsatz von Laub und Feinwurzeln (1.9 bis 5.6 tC/ha/yr für Eiche bzw. Esche mittlerer Bonität in Thüringen) unter anderem die Ernterückstände und die Wurzelstöcke aller geschlagenen Bäume (0.8 – 3.1 tC/ha/yr für Eiche bzw. Birke). Des weiteren zeigte eine Monte-Carlo-Sensitivitätsanalyse auf, dass die Genauigkeit der ermittelten Streueinträge (cv=14% für Buche bis 25% für Kiefer) stark erhöht werden kann, indem der Zusammenhang der Lebensdauer von Laub mit Umweltgradienten besser quantifiziert und in die Modelle integriert wird.

Der zweite wesentliche Fortschritt der Arbeit für die Initialisierung des Bodenmodells war die Einführung der vereinfachten Gleichgewichtsannahme und der Korrektur für transiente Zustände (Artikel IV). Schon minimale Verletzungen der strengen Gleichgewichtsannahme führten zu sehr großen Abweichungen in der Modellparameterisierung und den daraus resultierenden Initialisierungszuständen für das Bodenmodell. Die vereinfachte Gleichgewichtsannahme setzte nun nur ein Gleichgewicht für die Zustandsvariablen der schnell abbaubaren Ausgangsstoffe voraus, und nahm die langsamste Fraktion davon aus. Die Korrektur erniedrigte den durch die strenge Gleichgewichtsannahme ermittelten Wert für die am langsamsten abbaubare Fraktion mit Hilfe einer unabhängigen Schätzung der gesamten Boden-Kohlenstoffvorräte. Die Anwendung der Korrektur an einen Beispielbestand, an dem die Gesamt-Bodenvorräte gemessen worden waren, korrigierte den Kohlenstoffvorrat um 30%, was dazu führte, dass in Simulationen mit verschiedenen Szenarien von Streueintrag und Klimaentwicklung eine zusätzliche Kohlenstoffsenke von 5.7±1.5 tC/ha über 100 Jahre quantifiziert wurde. Für die Anwendung auf Ebene von Forstämtern oder Bundesländern wurden Boden-Kohlenstoffvorräte mit Hilfe von flächenhaft verfügbaren Daten und Regressionsmodellen für jeden Bestand geschätzt (Wirth et al. 2004).

Die vorgestellte Methodik ermöglichte es, die Kohlenstoffdynamik jedes einzelnen Bestandes ganzer Forstflächen zu simulieren, und dabei explizit die gemischte und geschichtete Struktur der Bestände zu berücksichtigen. Dem entgegen müssen andere Quantifizierungsansätze entweder einige intensiv untersuchte Standorte als flächenrepräsentativ für das Untersuchungsgebiet voraussetzen, oder sie müssen die vorliegenden Daten stratifizieren und von den spezifischen einzelnen Bestandesstrukturen abstrahieren. Mit dem vorgestellten Modell war es nun möglich, zu prüfen, ob diese Stratifizierung und Vernachlässigung von Details der Bestandesstruktur eine systematische Abweichung in der simulierten Kohlenstoffsenke bewirkt. Dazu wurde das Modell TreeGrOSS-C auf 1616 Einzelbestände des Forstamtes Hummelshein angewendet und die Resultate mit der Anwendung des Modells auf einen stratifizierten Datensatz verglichen (Artikel V). Auf der Ebene einzelner Bestände zeigten sich große Abweichungen des stratifizierten Ansatzes vom expliziten Ansatz in den simulierten Ökosystem-Kohlenstoffvorräten (-39% bis +38%), der Kohlenstoffsenke über 100 Jahre (-1.1 bis +1.9 tC/ha/yr) und Unterschiede in der Verteilung der Kohlenstoffvorräte zwischen lebender Baumbiomasse und Boden und organischer Auflage. Dies war vor allem auf die unterschiedlichen Eigenschaften und Parametrisierungen der eingemischten Arten im einzelbestandesweisen Ansatz zurückzuführen. Bei Entscheidungen zwischen verschiedenen Bewirtschaftungsmassnahmen für konkrete Bestände, wirkt sich die Art der Mischung und Schichtung der Bestände auf die Größe der Kohlenstoffsenke aus. Da die Ergebnisse des stratifizierten Ansatzes jedoch für einige Bestände in positiver und für andere Bestände in negativer Richtung von den Ergebnissen des expliziten Ansatzes abwichen, glichen sich die Unterschiede auf Ebene des Forstamtes aus. Dieses Ergebnis weist darauf hin, dass der stratifizierte Ansatz keine systematische Abweichung in der Quantifizierung der Kohlenstoffsenke mit sich bringt.

Die vorgestellte Methodik ist ein wichtiger Schritt in Richtung einer Unterscheidung direkter anthropogener und natürlicher Ursachen für die Kohlenstoff-Senke in Forsten. Die nächsten Schritte sind zum einen eine bessere Repräsentation der sich ändernden Umwelteinflüsse auf das Wachstum der Bestände. Zum anderen wird eine formellere Spezifikation der aktuellen Bewirtschaftung und des Waldumbaus benötigt, um einen realistischeren Bewirtschaftungsplan zu implementieren.

Thesis Frame

1. Abstract

Managed forests act as sinks or sources of atmospheric carbon by temporarily sequestering carbon in standing biomass, dead wood, organic layer, mineral soil, and wood products. Accounting of this carbon sink and managing forests with the aim of increasing the carbon sink need projections of the development of the sink with different management options. This thesis developed a methodology to simulate the carbon sink of individual managed forest stands using standard forestry data sources as they are available for many forested regions in Europe. As a test case area the German federal state Thuringia was taken in accordance with several other forest carbon projects. The presented methodology extends an empirical multi-species stand growth model with carbon quantification and couples this model to the Yasso soil carbon model, which was extended to handle multiple species and cohorts. The coupled model also includes newly developed component models of forest management, and of carbon in wood products.

The calculation and analysis of current carbon stocks in tree biomass, organic layer and mineral soil was based on established methods. Projecting the development of the carbon stocks, however, required further research on biomass equations for the tree compartments branches, foliage and root. The biggest challenge was to estimate the initial pool sizes of the soil carbon model that strongly depend on site history. One part of the solution was the introduction of the relaxed equilibrium assumption, which assumes that all pools are near equilibrium unless the pool with the slowest turnover. This assumption allowed to infer initial states by average past soil carbon inputs and by an estimate of current soil carbon stocks. A second part of the solution was to model average soil carbon inputs of the former century by using a combination of yield tables and the stand growth model.

In addition to the prediction of mean carbon stocks and their changes I focused on their uncertainties and error propagation on upscaling. I found that the precision of tree biomass carbon stocks is strongly overestimated if site quality and correlations between tree biomass at similar site conditions are not carefully accounted for. Litter inputs to the soil and hence also soil carbon stocks strongly vary with lifetime of foliage and branches, which vary with site conditions. Additionally, if a soil carbon pool with very long turnover time is considered, the long term dynamics of the soil carbon sink is determined by the site history. I conclude that differences in site quality and site history must be adequately accounted for to avoid bias in the estimate of the carbon sink at forest district scale.

The developed methodology made it possible to simulate the carbon sink of each individual stand of entire forest areas. A comparison of the model application to the Hummelshein forest district in Central Germany with a stratified approach showed that multi-cohort and multi-species stand properties have a high impact on carbon dynamics at stand scale but that they are levelled off at forest district scale. The presented methodology is a move towards factoring out natural and anthropogenic effects on the forest carbon sink. Next steps in the development of the approach are a better representation of environmental conditions in the stand growth component model and a more formal specification of changes in forestry management.

2. Introduction

Projections of the effects of forestry management on forest carbon dynamics are important to factor out direct anthropogenic effects versus indirect, natural, and historical effects (Lasch et al. 2005, Vetter et al. 2005, Albani et al. 2006) as required by the Kyoto Protocol (UNFCCC 1997). In the past, research has focused on quantifying the forest carbon sink at stand scale (DeAngelis et al. 1981, Ellenberg et al. 1986, Aubinet et al. 2001, Curtis et al. 2002, Valentini 2003) and at national to continental scale (de Wit et al. 2006, Liski et al. 2006, Ågren et al. 2007). Projections of management effects at the forest district scale are rare, even though decisions on forest management are made at this scale, and also activities to improve the carbon sink strength of forests would take place at district scale. In Germany, Lasch et al. (2005) applied the physiological 4C model to long term research plots in order to investigate effects of management on carbon sequestration and ground water recharge at regional level. However, their model requires detailed input data and parameters, which makes it difficult for application in management enterprises. In forestry empirical models are used more frequently (Hasenauer 2006). These empirical models are usually based on tree properties and have no explicit representation of the carbon cycle and environmental changes. In Finland, Matala et al. (2006) were able to extend the empirical Motti model by relative variations in volume increment with increased temperature, carbon dioxide concentrations and nitrogen depositions inferred by a physiological model. Nuutinen et al. (2006) incorporated the growth differences into a large-scale forest scenario MELA model, which then was applied to national forest inventory data. I pursued a similar approach of extending an empirical model. I simulated the carbon sink at forest district level based on standard forestry data by adapting the stand simulator TreeGrOSS (Nagel 2003) to work with standard forest inventory data and coupling it with carbon calculators, a management planning model, a soil carbon model, and a wood product carbon model.

3. Objectives

The main objective of this work was to develop a methodology to simulate the carbon sink of a managed forest ecosystem using standard data sources, which are easily and commonly available.

This main objective can be refined to the following specific objectives.

- To calculate and analyse current carbon stocks in living tree biomass, organic layer, and the mineral soil using standard forestry data sources (Publication I)
- To select or develop a stand growth model that is driven by standard forestry data sources and that is able to explicitly represent different thinning strategies (preparatory work for Publications II-V).
- To extend the stand growth model to provide outputs in carbon units. This involves estimation of carbon stocks in tree biomass compartments foliage, branches, and root (Publication II)
- To extend the tree biomass carbon model to a complete forest carbon model including deadwood, organic layer, mineral soil, and carbon in wood products (preparatory work for Publication V).

The fourth specific objective required to infer initial states of different soil carbon pools, which depend on disturbances and carbon inputs during former centuries. This challenge was tackled by two Publications.

- Publication III calculates average carbon inputs to the soil using a combination of yield tables and the stand growth model.
- Publication IV explores the consequences of the case where soil pools are apart from equilibrium and develops the concept of the relaxed equilibrium assumption and the methodology of the transient correction, which attempts to account for unknown past disturbances.

Finally, I was interested, if the application of the developed method at forest district scale would improve projections that are based on aggregated forest data (Publication V).

4. Background

This section briefly introduces the main concepts and terms that are used in the discussion about forestry management and modelling the forest carbon sink.

4.1. Terrestrial carbon cycle

The terrestrial carbon cycle together with the most important flows and terms according to Schulze et al. (2000) is shown in Fig. 1. During photosynthesis atmospheric carbon is used to synthesize carbohydrates (Gross Primary Production GPP). A part of this carbon is respired by the plant (authothrophic respiration R_a) and the remaining carbon is used to build up biomass (Net Primary Production NPP). Most of the carbon in foliage, branches and roots is turned over by litter production and enters the organic layer and the mineral soil as soil organic matter (SOM) or dead biomass. The SOM and dead biomass is consumed by micro-organisms and partly respired (heterotrophic respiration R_h) and partly transformed to more recalcitrant forms of SOM, which can reach an age of thousands of years (Martel and Paul 1974, Rumpel et al. 2002). The stabilization mechanisms are still in debate (Sollins et al. 1996, von Lützow et al. 2006). The small difference between production and respiration describes the net change of stocks at the site (Net Ecosystem Production NEP). During

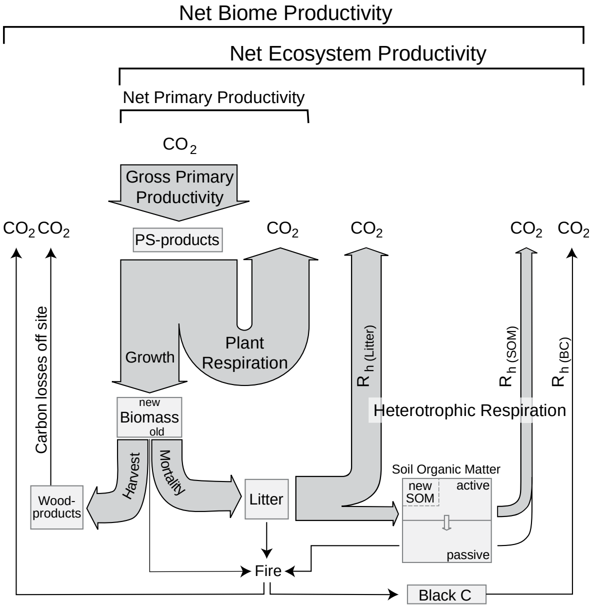


Figure 1: Fluxes and terms of the terrestrial carbon cycle according to Schulze et al. (2000)

thinning and harvesting operations a part of the carbon is exported from the ecosystem and used in fuel or wood products. In several ecosystems also fire plays an important role. Harvest and fire are captured on larger space and time scales with the term Net Biome Production (NBP). The above terms can have slightly different meanings when concerning different carbon quantification methods and refinements of these terms can be found in (Chapin et al. 2006).

4.2. Thinning strategies and yield tables

Foresters can influence the forest carbon balance mainly by selecting tree species and by cutting trees. In some regions also fertilization or controlling fire are common management activities which affect the carbon balance (Nabuurs and Schelhaas 2002, Schoene and Netto 2005, Jandl et al. 2007a). In Central Europe most of the forests have been managed as even-aged, mono-species plantation. The final cut of all trees is called clear cut or final harvest and an intermediate cut of single trees, which promote the growth of the remaining trees, is called thinning. The foresters decide first, about the times to thin or harvest trees, second, how much timber volume to thin, and third, which trees to select for thinning. With precommercial thinning all cut trees are left at the site and with commercial thinning a part of the cut trees is removed and used. The three most common approaches of selecting trees in Central Europe were thinning from below, thinning from above, and crop tree thinning. With thinning from below, only the suppressed trees with a diameter below the average are selected for cutting. With thinning from above, also some dominant and co-dominant trees are cut. With crop tree thinning, some dominant trees are marked to remain until final harvest and competing trees around them are cut gradually.

A model for managing even-aged stands that maximises merchantable timber production is recorded in yield tables. In general, yield tables describe the ‘‘regular growth’’ of forest stands for: (1) distinct tree species; (2) under constant environmental conditions; (3) according to a defined management regime. Each table lists stand ages and the expected stand attributes: stand age (yr), dominant height (m), basal area (m^2), tree number per hectare (1/ha), and timber volume (m^3/ha), quadratic mean of tree diameters at breast height (dbh) (cm), and stand height (m). Different tables in one collection describe different growth patterns. They are distinguished by the absolute site index: the expected height of trees (m) at stand age 100 years (Kramer and Akça 1995). Yield tables are only applicable to even-aged monospecific stands and because of environmental changes over the last 50 to 60 years some older yield tables do not reflect current tree growth (Mund et al. 2002, Jandl et al. 2007b).

4.3. Tree growth models

With the change of forest management goals to several forest functions besides timber production, forest management shifts from even-aged monospecific stands towards uneven-aged mixed species stands (Larsen and Nielsen 2007). Because stand structure and competition of trees for light and other resources have a large effect on tree growth, the growth of single trees has to be modelled in order to predict the growth of such uneven aged stands. A good introduction into the concepts of tree growth models can be found in Hasenauer (2006). Usually, these models predict diameter and height growth for each tree. The increment functions are based on a potential growth, which depends on species and site conditions and which is decreased by the competition between trees. Alternatively, the increment is estimated directly from the tree properties and site conditions. Different competition indices have been developed which can be classified into distance dependant ones and distance independent ones. For the first case, the exact position of each tree within the stand is required. The distance independent indices are based on a mean distance between trees on a plot. Often, the competition indices require a description of the crown form of several species by crown models. In addition to diameter and height increment, most of these models can also predict mortality and regeneration. The calibration of tree growth models requires an extensive set of repeated tree observations that are usually collected at permanent research plots. The models are classified as empirical models, because they describe observed increment data without explicitly modelling the structure of the increment process, i.e. photosynthesis and biomass allocation. In comparison, process-oriented physiological models explicitly represent these processes. They are regarded more successful in predicting changes with changing environmental conditions. However, they require much more data on application and often focus on natural vegetation. Gap-models (Botkin et al. 1972, Bugmann et al. 1997, Seidl et al. 2005) are the class most similar to the empirical tree growth models. A classification of further forest growth models can be found in (Porté and Bartelink 2002).

All dynamic models are based on various assumptions and simplifications. A model can be viewed as a tool to calculate several outputs for the given assumptions. Therefore, I use term “projection” instead of “prediction”. The two most important simplifications in this study are first, the assumption that tree growth as observed during the last century does not fundamentally change during the next century and second, the assumption that management was and is guided by yield tables.

4.4. Modelling and simulation (M&S)

A model is an abstraction of a system and can be specified at different hierarchy levels (Zeigler et al. 2000). While regression models work on the input/output function level, dynamic models additionally describe the history and internals of the system by the systems state. It is important to distinguish between first, the real system, second, the experimental frame, which constrains the real system to several properties by specifying the observed inputs and outputs including their time resolution, third, the model, which specifies the rules and equations of the modellers abstraction and fourth, the simulator, which numerically executes the model over time and generates a trajectory of outputs for given inputs. The three most common modelling formalisms of describing system dynamics are first, fixed time steps (DTSS: discrete time step specified system), e.g. computer clock ticks, second, times of events (DEVS: discrete events specified system), e.g. processing and waiting times in queuing lines, and third, differential equations in continuous times (DESS differential equation specified system), e.g. the movement of a satellite in orbit. A DESS can be approximated by a DTSS by quantizing the time axis or by a DEVS by quantizing of the state space (Kofman 2003, 2004). There are different simulators for different modelling paradigms. In many environmental model implementations, the distinction between model and simulator is not clear. This prohibits the distinction between model verification and validation, i.e. the check that the model is correctly executed versus the check that the model correctly describes the experimental frame. Models that are specified a higher hierarchy level also describe the decomposition of the system into smaller subsystems and the interactions between these subsystems. Reynolds and Acock (1997) pose advantages and requirements to such component models. One of the most important requirements is that component models communicate by inputs and outputs only. The parallel DEVS formalism (Chow 1996, Zeigler et al. 2000) supports a hierarchy of coupled models. Both atomic and coupled models specify input and output ports, and a coupled model specifies how these ports are connected. The simulator takes care that the outputs of one component model are delivered to the input ports of the corresponding component model. Such a communication between models is called a message.

5. Materials and methods

5.1. Study region

The focus of this study is the managed forest in Thuringa, a federal state in Central Germany (Fig. 2). This region had already been selected for a study on implementing the Kyoto protocol in Germany (Wirth et al. 2004, Mund et al. 2005) and as a test area for the European-wide Carbo-Invent carbon inventory study (Baritz 2005). The largest parts of the 540 000 ha forest area are found in the southern low mountain ranges, where geology is dominated by slate, and in the limestone dominated areas in the east and west. The soils of the central Thuringian basin are covered with a loess layer. Hence the fertile soils of the basin are used mainly for agriculture and only 4% of the area is forested. Soil is dominated by dystric cambisols, however there is a mosaic of various bedrocks and soil types at the scale of 1’ ha.

The climate of Thuringia is characterized by the transition from maritime Western Europe to the continental Eastern Europe (Fig. 3). Temperature and precipitation change with increasing elevation in the mountain range and there are also foehn wind effects.

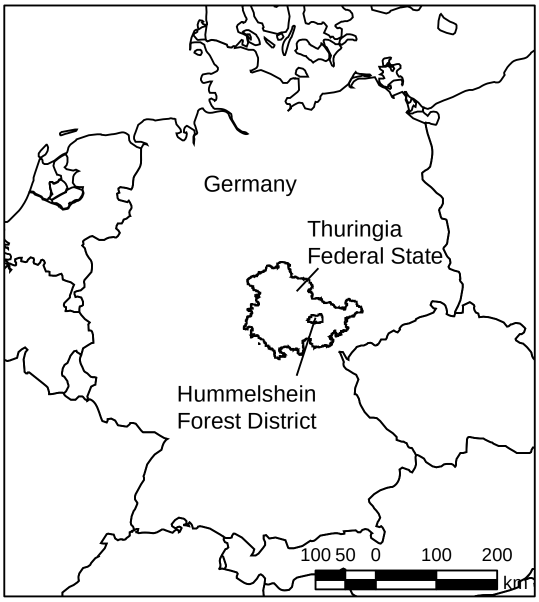


Figure 2: Map locating the study area.

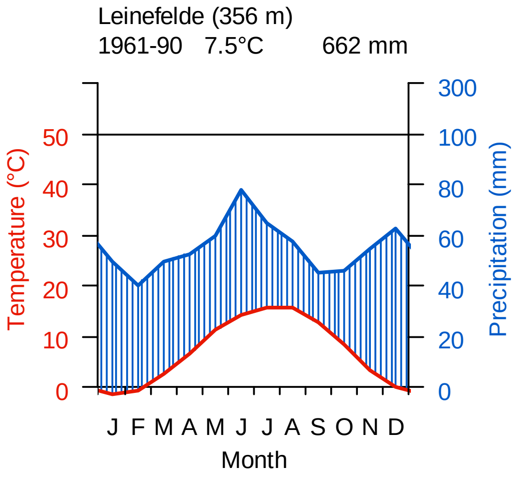


Figure 3: Climate diagram of a weather station in the west of the Thuringian basin. Data Source: Deutscher Wetterdienst (1961-90)

The single Publications focus on different extents. Publication I utilizes soil catena measurements of the Tharandt forest east of Thuringia, the validation sites are distributed across the forest area of Thuringia, Publication II develops biomass equations that are applicable to entire Central Europe including Thuringia, the sites of the application examples of Publications III and IV are located in the west of Thuringia, and the forest district Hummelshein of Publication V is located in the east of Thuringia.

5.2. Forestry

After the last glaciations, the entire area was initially populated by early sucessional species (poplar, birch, willow, spruce). The naturally dominating species of later states of succession are spruce (*Picea abies*) at the higher elevations, beech (*Fagus sylvatica*) at the lower elevations with enough moisture, and pine (*Pinus sylvestris*) and oak (*Quercus spec)* at areas with not enough moisture for beech. Until 1300 most of the fertile soils in non-steep terrain were converted to agriculture and big parts of the remaining forest were used for wood pasture and extraction of litter for fertilizing agricultural land. Hence most of the forest soils were depleted in carbon. Around 1800 forests started to be regularly managed. Since then coniferous trees have been favoured, and in second half of the 20th century 70% of the forest area was dominated by conifers, mainly monospecific even-aged spruce stands. The management was guided by yield tables, which listed expected timber diameter, height, and volume of stands for different site qualities. The aim of nowadays forestry is to foster mixed and multi-cohort stands that are closer to the forests that are expected to occur naturally, if the grazing pressure of deer can be controlled.

5.3. Inventory data

Forestry administration of the German federal state Thuringia performs an inventory of timber volume for each stand every 10 years. The inventory is based on assessment of basal area and tree height of each stand with a relascope and provides information on cohorts, this means homogeneous groups of trees. The data includes species, age (year), quadratic mean of diameter at breast height (dbh) (cm), height (m) (calculated from stand height curve for given dbh), timber volume (m^3/ha), and basal area (m^2/ha). The inventory does not contain the variance of tree parameters, timber volume of trees with a dbh smaller than 7cm, nor the number of trees within a cohort.

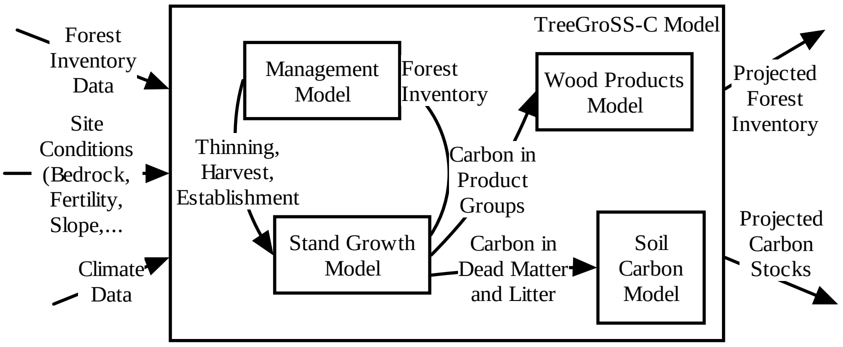
In 1960, forestry administrations of Eastern Germany started an inventory of site conditions (Kopp and Schwaneke 1991). The raw data of the soil profiles have been aggregated and classified to site classes. A site class consists of the categorical site parameters of climate/topography, parent material, water regime, nutrient availability, and moisture index. In that inventory, the parameter parent material is a combined description of topography, soil type, and bedrock.

5.4. Empirical equations of carbon stocks

Carbon stocks in whole tree biomass were calculated by multiplying timber volume of the forest inventory with an age- and site-specific factor. This factor is the product of wood density, an expansion factor from timber to entire tree biomass and the carbon contents. Factors for the dominating species Norway spruce (*Picea abies*) and Common beech (*Fagus sylvatica*) have been developed by the study of (Wirth et al. 2004). For pine (*Pinus sylvestris*) I used factors from (Lehtonen et al. 2004a). Tree biomass carbon stocks of other broadleaved species than beech were calculated using the factors for beech, and biomassof other coniferous species than spruce using the biomass-expansion factors of spruce but species-specific wood density and carbon content according to (Weiss et al. 2000). Carbon turnover was calculated by applying conversion-expansion factors for several tree biomass compartments and a mean turnover rate. For a more detailed description of the turnover rates see Publication III.

Current carbon stocks in mineral soil and organic layer were calculated using the inventory of site conditions, the dominating tree species and the empirical functions of Wirth et al. (2004).

Figure 4: Conceptual view of the TreeGrOSS-C model. Arrows denote inputs and outputs to the TreeGrOSS-C model and its component models.



5.5. The TreeGrOSS-C coupled model

The coupling of a stand growth model, a management model, a soil carbon model, and a wood product model resulted in the model TreeGrOSS-C (Fig. 4). While the stand growth model has a discrete time step of five years, the other two models are described by continuous differential equations. Instead of approximating the solution of the differential equations by a time-stepped approach, I used the quantized approach (Kofman 2003). This approach provides exact control on the accuracy of the carbon stocks and allows for time steps up to thousands of years near the equilibrium. The Yasso model was implemented using the computer language C++ and coupled to the other models, which are implemented in Java, using the DEVS-abstract model (Wutzler and Sarjoughian 2006). The submodels communicate solely by messages which are routed in time order between output- and input ports.

5.6. The TreeGrOSS stand growth model

The TreeGrOSS (Tree Growth Open Source Software) model (Nagel 2003) is a public domain variant of the BWinPro model (Nagel et al. 2002). According to the classification of Porté and Bartelink (2002) it belongs to the class of non-gap distance-independent tree models. The empirical model is based on a growth and yield experiment data pool of about 3500 plots in northern Germany. It uses the potential growth concept, which reduces species and site dependent maximum diameter and height growth of single trees by their competition situation (Hasenauer 2006). Both, a distance dependent and a distance-independent calculation of competition indices are supported. In this work the distance-independent variant was used, because it uses only a mean distance within a plot and does not require tree coordinates. The TreeGrOSS model includes a generator of tree diameters (dbh) based on the Weibull function (Nagel and Biging 1995). In order to adapt the model to the available inventory data, I extended the model by the concept of cohorts and developed modules that read and write inventory records to a database. Further, I extended the model by thinning routines, which selected trees randomly from a probability distribution of the tree diameter. Eventually, I used one side of a Gaussian distribution with a mean of cohorts minimum or maximum diameter respectively and a standard deviation, so that the basal area equalled the specified basal area of thinned trees (Fig. 5). The model and the extensions were validated against plot data of several permanent sampling inventories of both monospecific and multi-cohort multi-species stands within the study region. The complete time series, which partly covered more than 100 years, were kindly provided by the Eberswalde forestry research institute and the chair of Forest Growth and Timber Mensuration at TU-Dresden and preprocessed by Mund et al. (2005).

5.7. The Yasso soil carbon model

The soil carbon model Yasso was designed by Liski et al. (2005) in order to model soil carbon stocks of mineral soils in managed forests. Figure 6 displays the model structure and the flow of carbon. The colonization part (Fig. 6a) describes a

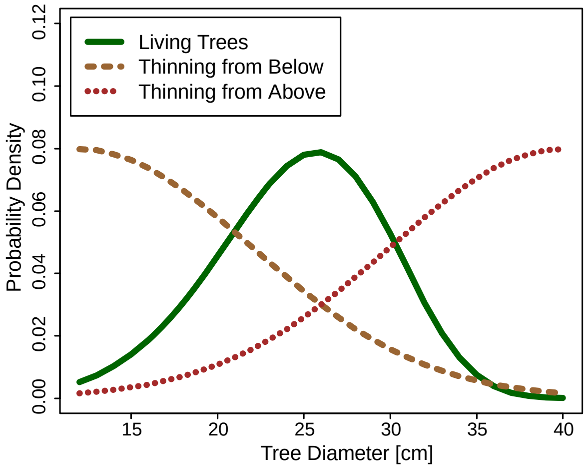


Figure 5: Selecting trees for thinning in the model by a probability distribution of tree diameter

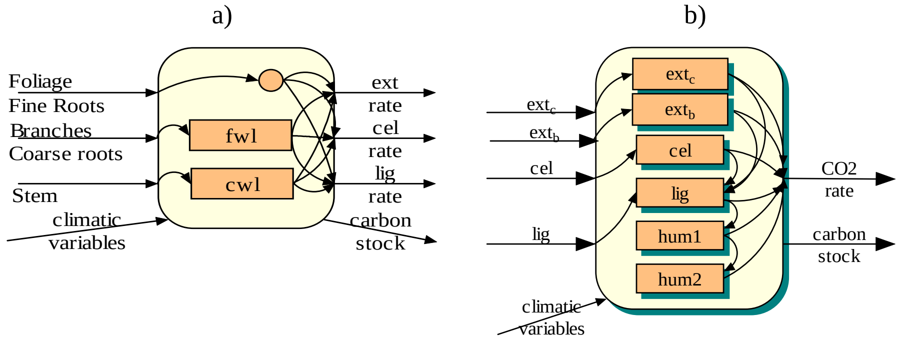


Figure 6: Flow chart of the Yasso model. a) species dependent part of litter colonization and separation of litter into chemical compounds b) species independent part of decomposition of chemical compounds

delay before decomposers can attack the parts of the woody litter compartments and additionally describes the composition of the different litter types of compartments that correspond to the kinetically defined pools. The decomposition part (Fig. 6b) describes the decomposition of the chemical compounds. The fwl-pool can be roughly associated with undecomposed litter, the cwl-pool with dead wood, and all the other parts with organic matter in soil including the organic layer. The decay rates are dependent on mean annual temperature (or alternatively effective temperature sum) and a drought index (difference between precipitation and potential evapotranspiration during the period from Mai to September). In the standard parameterization the decay rates of the slower pools are less sensitive to temperature increase than the fast pools (humus one: 60%, humus two: 36% of sensitivity of fast pools). The model has been tested and successfully applied to boreal forest (Peltoniemi et al. 2004), litter bag studies in Canada (Palosuo et al. 2005), and as part of the CO2FIX model all over Europe (e.g. Nabuurs and Schelhaas 2002, Kaipainen et al. 2004). In order to simulate multi-species stands I duplicated and parameterized the colonization part for each tree cohort and coupled all the duplicates to the single species independent decomposition part.

The soil pools were initialized by spin-up runs with repeated climate data of the last century and average soil carbon inputs. The average soil carbon inputs were derived for each species by simulating the stand growth model over an entire rotation cycle including final harvest (Publication III). Soil carbon inputs for cohorts, i.e. tree groups, in multi-cohort stands were decreased by the proportion of tree groups basal area to stands basal area. In order to account for soil degradation in the past, I reset the slowest pool after the spin-up run so that the sum of pools match the carbon stocks that were obtained by spatial extrapolation of observed carbon stocks using the dominating tree species and site conditions (Publication IV).

5.8. The products carbon model

The products carbon model simulated the residence of carbon in wood of different groups of wood products. The simple model assumed that the carbon stored in forest products is released to the atmosphere again right after the product is out of use. Hence it did not account for recycling of wood products. Dumping of wood in landfills was not considered, because this has been forbidden by a law of waste products in Germany. One basic model assumption was that the portion of wood products that goes out of usage is the reciprocal of the average lifetime of the product (Eq. 1).

$$\frac{\delta C_p}{\delta t} = \frac{1}{t_{lifetime,p}} \cdot C_p$$

Where C_p is the pool size of product pool p and $t_{lifetime,p}$ is the average time of product use (Table 1). Hence the carbon pool of each product group is described by a first order exponential decay (Eq. 2).

$$C_p = C_{p,-\Delta t} \exp\left(-\frac{1}{t_{lifetime,p}} \cdot \Delta t \right) \qquad \text{(Eq. 2)}$$

Where Δt is the time that passed since last input and $C_{p,-\Delta t}$ is the former pool size.

In order to couple the stand growth model to the product model, the simulated removed timber had to be allocated to the different product pools. In a first stage, the wood volume was allocated to different sale segments by species and mean basal area diameter based on assortment tables (Schöpfer and Dauber 1985, Schöpfer and Stöhr 1991). Next, these sale segments were allocated to the different product groups based on an analysis of the first stage of wood processing (Profft et al. 2007). Losses by sawing and leaching were allocated to the most short-lived class. I used the resulting shares of timber volume to allocate the simulated carbon in removed timber to the product groups of the products carbon model.

The product carbon model was implemented in the following way. Whenever wood was extracted from a stand, the amount of carbon in harvested timber corresponding to the different product groups was calculated and assigned to the inputs of the product carbon model. Next, the pools of each product pool were updated by Eq. 2. Finally the inputs were added to the corresponding pools, and the sum of all the pools was calculated.

Initial stocks of the products were based on (Mund et al. 2005) Table 2.9, which presents harvest statistics of 195000 ha Thuringian forest area over the years 2001 and 2002.

Table 1: Wood product classification by average lifetime, i.e. time of product use, based on (Wirth et al. 2004).

Product class	Products	product life time [years]	Main class
energy	fuelwood, slash, non-commercial wood,	1	Wood products with short lifespan
pulp	pulpwood small poles, wood for packing material, wood for temporary constructions (building sites)	3	
pallets	pallet wood, poles, ram piles	11	
panels	furniture, particle board, chipboard, fibreboard, etc.	25	Wood products with long lifespan
sawn parquet	parquet wood	43	
sawn timber	construction wood	51	

5.9. The forestry management model

The outputs of the forestry management model were information on thinning at several stand ages, final harvest, and establishment of new cohorts. The dynamic behaviour of the product model was separated from the management plan component (Fig. 7).

For each stand age listed in the management plan, the management component model issued an output message, which demanded a stand inventory. The coupled model routed the message to the stand growth model, which in turn generated an output message containing the current stand inventory. When the message with the stand inventory arrived at the input port of the management model, the management plan component specified the target basal area and the target diameter for thinning events. Currently, only a yield table-based version of a management plan has been implemented. The target basal area and the target diameter of each cohort were interpolated by yield tables for the cohort age. Yield tables refer to monocultures; hence the target was multiplied by the share of basal area of the tree group within the stand. Finally, the thinning type (precommercial / commercial / harvest), the basal area of all thinned trees, and the basal-area-mean diameter of the thinned trees was calculated by the difference between the inventory and the target. The amount of stem volume that is removed by a single thinning operation was constrained not to exceed 20% of the basal area to avoid instability of the stand.

In addition to messages with thinning information, the management model generated output messages for harvest and establishment of new cohorts. After each clear-cut, cohorts were established that shared the basal area in the same proportions, as the cohorts did at the start of the simulation. Both yield tables and the carbon accounting model were not tailored to simulate growth of very small trees. Therefore the yield-table based management plan established the stand when the dominant cohort had reached a diameter at breast height of 7 cm. The stand age corresponding to this diameter was estimated from yield tables. The absence of biomass and biomass turnover in the first years after harvest, when diameter of the new dominant cohort was small, led to an underestimation of soil carbon inputs. However, this bias was small compared to mean carbon inputs across the rotation period.

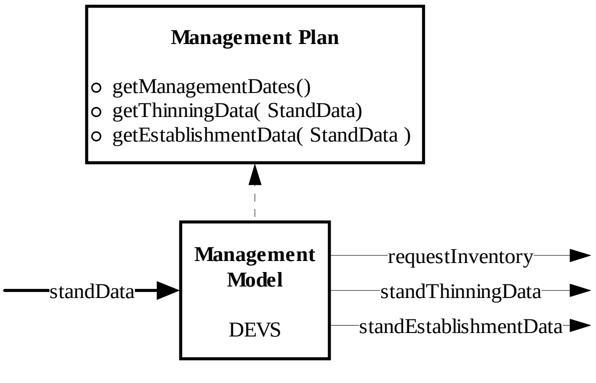


Figure 7: Input/Output relationship of the management component model.

5.10. Uncertainty analysis

Many parts of the model were constructed in a way that a relative deviations for parameters or for intermediate results could be specified with invocation of the model. In a Monte-Carlo analysis, these relative deviations were sampled from the assumed joint probability distribution of the parameters and intermediate results and the model was called several thousand times. The empirical distribution of the model outputs then was used to assess the uncertainty of the model outputs. Crucial to this approach are the assumptions about the variability of the model parameters. In the development of biomass functions (Publication II), I used mixed-effects models to assess different components of uncertainty. These components were crucial to scale the variance of biomass predictions up to the stand level, for which the uncertainty of the conversion-expansion is specified, which in turn propagates to the results of the Monte-Carlo analysis in Publication III.

6. Results and discussion

6.1. Carbon stocks (Publication I)

The combination of standard forest inventory data and data of site conditions was sufficient to quantify carbon stocks of tree biomass and the organic layer explicitly at stand scale. Contrary, standard forestry data was not sufficient to quantify carbons stocks in mineral soil and additional data was required. In addition to former carbon quantifications in Germany, which quantified similar carbon stocks in living tree biomass (10.0±0.1 kg/m^2), organic layer (3.0±1.4 kg/m^2), and mineral soil (7.3±1.4 kg/m^2) (Baritz and Strich 2000, Karjalainen et al. 2002, Wirth et al. 2004), I focused on the spatial distribution of the different carbon stocks at stand scale. This allowed for comparing different factors that influence carbons stocks. Stronger thinning intensities significantly decreased living tree biomass carbon pools. However, I did not find significant effects of site conditions on tree biomass carbon pools within the same climate.

6.2. Validation of the stand growth model

The validity of the TreeGroSS model for growth conditions of Thuringia was checked with data of permanent sampling inventories. The TreeGrOSS stand growth model was able to model diameter and basal area of monospecific stands as good as or better than local yield tables. In the case of multi-cohort and mixed stands the model matched the observed growth much better than applying local yield tables to a conceptual split of the stand into pure stands (Fig. 8). The TreeGrOSS model accounts for the decreased growth due to the competition state of the trees of the suppressed cohort. The yield table approach cannot account for this competition. There were still sometimes high relative errors for suppressed cohorts; however, the absolute amounts within the stands were small. Also the simulated growth of ash (*Fraxinus excelsior*) was slightly biased to higher values, but could be neglected as the share of Ash among tree species of the study region was very small. The change of the diameter during different thinning strategies was well represented by the thinning routines. This confirms that describing the selection of trees to be thinned based on diameter distributions is a suitable model approach (Lasch et al. 2005).

6.3. Uncertainty of converting tree properties to tree compartment carbon stocks and turnover (Publications II and III)

For Spruce and Pine I found suitable biomass functions, biomass expansion factors, basic wood density, and carbon contents in the literature for all major tree compartments, which were necessary to extend the TreeGrOSS model to provide outputs in carbon units. For Beech, however, there was no consistent set of biomass functions, aside from above ground and total tree biomass. Therefore, I developed biomass functions of other major tree compartments by a meta-analysis of original tree measurements from

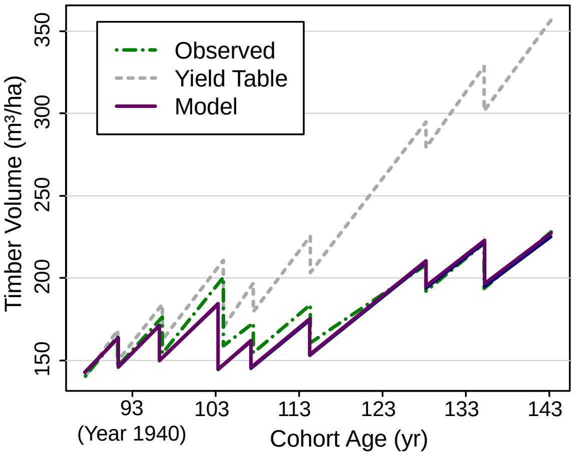


Figure 8: Comparison of timber volume from a suppressed beech cohort of the permanent inventory plot Leinefelde 245 (data from Eberswalde forestry research institute) to model predictions by yield table (Dittmar et al. 1986) and predictions of the TreeGrOSS model.

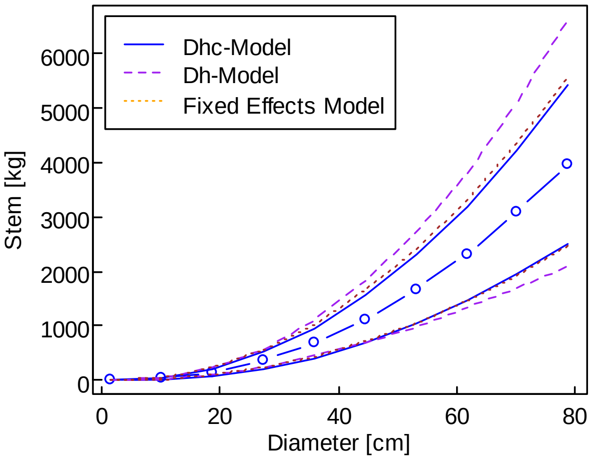


Figure 9: 95% confidence intervals of stem biomass for different forms of modelling variation between groups. The fixed-effects model does not account for the differences between studies. The dh-model accounts for these differences by random effects. The dhc-model also accounts for these differences by random effects but explains these differences in part by additional covariates. It can be seen, that the mean predictions do not differ, but the confidence intervals of the predictions differ. The confidence band for the fixed-effects model is too narrow because it does not account for the differences between the studies, neither implicit by random effects nor explicit by covariates.

13 studies. The approach of using non-linear generalized mixed effects model allowed the separation of variation due to residuals and differences between studies, i.e. specific site conditions, provenances, etc. (Fig. 9). The means of the predictions of the presented biomass equations of stem and foliage agreed well with other published biomass functions for Common Beech in Central Europe (Bartelink 1997, Le Goff and Ottorini 2001, Cienciala et al. 2006). However, I predicted larger uncertainties of tree biomass compartments than those supposed by former quantifications basing on smaller datasets only. In addition to these uncertainty considerations at tree level, I showed that it is also important to consider covariances between single tree biomass predictions at stand level. This role of covariances was already demonstrated by Lehtonen et al. (2004a, 2007), but in this study I developed theory and practical tools to actually quantify the covariances.

The turnover of carbon of the major tree compartments foliage, branches, and fine roots and quantification of harvest residues was used to quantify litter production, i.e., the carbon flux to the forest floor. In conjunction with modelling past mean average litter production for soil carbon initialization, I performed a Monte-Carlo sensitivity analysis of the model parameters. The analysis calculated an importance index. A high importance index indicates that parameters have both, a low precision and a high sensitivity in respect to the studied model outputs. The parameters with the highest importance index were associated with branch and foliage turnover (Fig. 10). I note that in the model, the litter below ground litter production was estimated by a species-specific fraction of the above-ground litter production, and not by the usual approach of calculating fineroot biomass and turnover. Hence, in order to decrease uncertainties of the used model, a better description of the dependency of foliage and branch turnover times on site conditions as water and nutrient availability or temperature are required. Several Scandinavian studies already related foliage and branch turnover to tree properties or environmental gradients (Lehtonen et al. 2004b, Muukkonen and Lehtonen 2004, Ågren et al. 2007). In Germany there are studies of foliage lifetime related to forest decline (e.g. Wachter 1985). Similar studies should be initiated for several regions and species and their results should be incorporated in carbon turnover calculations.

6.4. Litter Production and Initial soil model carbon pools (Publications III and IV)

In order to model changes in forest ecosystem carbon stocks, the initial state of all carbon pools

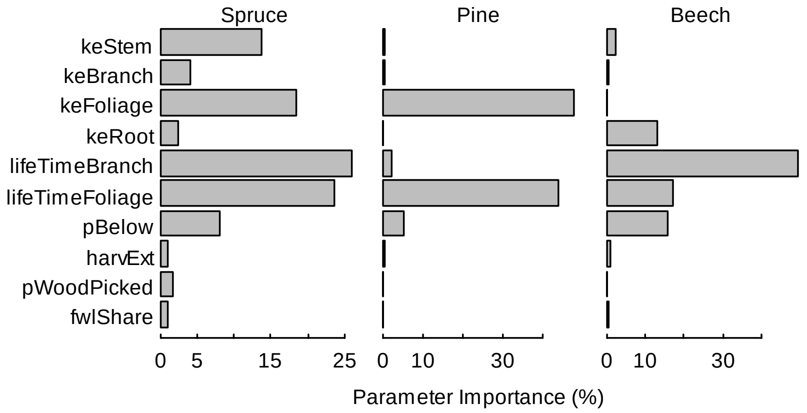
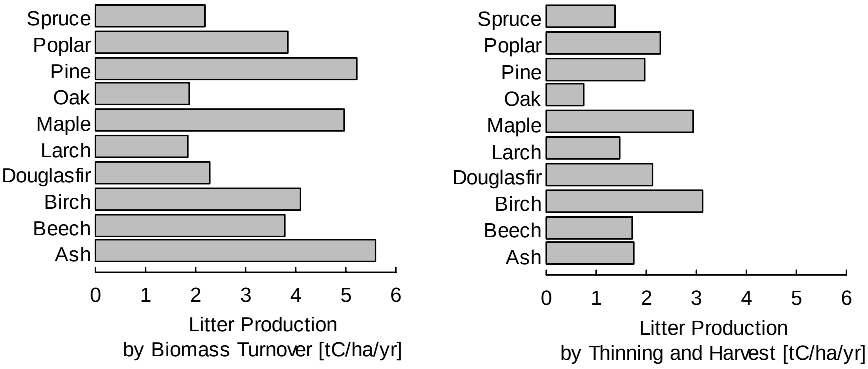


Figure 10: Importance index, i.e. relative influence of the parameter uncertainty on the results uncertainty, for litter production of intermediate site quality. For all species the mean lifetime of foliage is very important. Uncertainty in information on harvest (last three parameters) is not contributing much to the uncertainty in results in all three cases.

Figure 11: Litter production of monospecific stands of medium site quality.



in the model has to be specified. For the conceptual pools of the soil model the initial stocks of these pools had to be estimated. This is usually done by a spin-up run of the model, which assumes the initial stocks of the pools to be near equilibrium with mean carbon inputs. In order to derive mean past carbon inputs to the soil model and to the wood product model, I simulated stand development of monospecific stands and aggregated the simulated litter production by turnover of foliage, fine root, and branches, harvest residues of fine wood, coarse root, and coarse wood across the entire rotation period (Fig. 11). The increase of litter production with site quality was of the same magnitude as the mean of the litter production and the differences between species (3-8 tC/ha/yr). Therefore, regional studies of carbon quantification should properly account for this fact, possibly by stratifying the studied area for different site qualities. The productivity also explains why I quantified a larger litter production for pine (7.2 tC/ha/yr) than a finish study (Peltoniemi et al. 2006). Further, I quantified the uncertainty of the calculated litter production, which strongly depended on the assumptions of the uncertainty of the model parameters. The uncertainty for pine (cv=25%) was higher than in the study of Peltoniemi. This can be mostly attributed to the single parameter foliage turnover, for which I assumed a higher uncertainty (cv=25%).

The mineral soil contains carbon of age up to thousands of years. I posed the hypothesis that the soil model carbon pool which represents this old carbon does not reach equilibrium with mean soil inputs shortly after severe disturbances, and that therefore many soils in Central Europe are still recovering from former agricultural use, wood pasture, or litter removal. There is strong evidence from case studies for the persistence of intensive disturbances, such as forest fires (Parker et al. 2001, Wardle et al. 2003) and erosion (Hedges et al. 1997, Polyakov and Lal 2004). Therefore, I suggested and applied the transient correction, which decreases the stock of the slowest pool after the spin-up run, so that the sum of soil carbon stocks matches an independent estimate of soil carbon stocks. The application of the transient correction at the Leinefelde chronosequence in the west of Thuringia decreased the spinup-run predicted carbon stock by 30% which resulted in an additional carbon fixation of 5.7±1.5 tC/ha within 100 years consistently across scenarios of different litter inputs and climate change (Fig. 12). The transient correction can be applied at forest district scale, where the independent estimate of carbon stocks is taken from extrapolating measured soil carbon stocks by regression models that estimate carbon stocks based on information obtained from stand map, forest inventory and the map of site conditions (Wirth et al. 2004).

6.5. Application at forest district scale (Publication V)

The integration of all the formerly presented

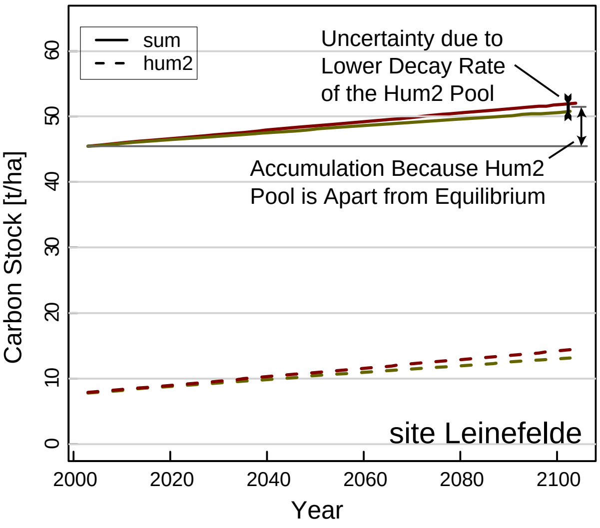


Figure 12: Development of the soil carbon stocks at the Leinefelde site. *sum* represent the sum of the stocks of the Yasso soil pools (ext+cel+lig+hum1+hum2). Hum2 is the slowest pool only. The lower ones of the diverging lines are trajectories of the simulation with standard parameterization of the slowest pool decay (k_{hum2} = 1.20e-3) and upper ones of a much lower value (k_{hum2} = 1.92e-06).

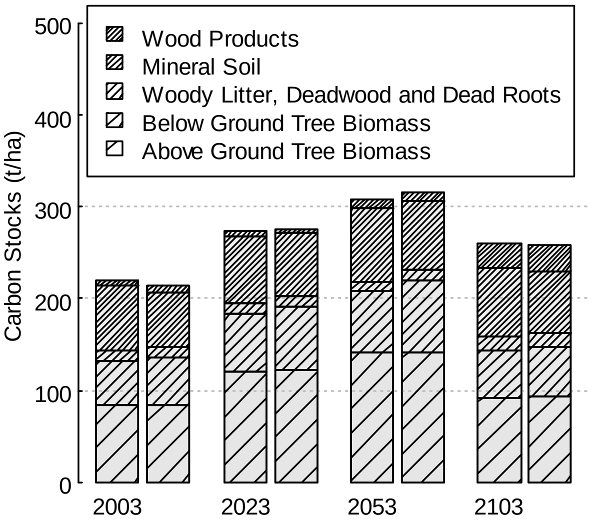


Figure 13: Projections of carbons stocks for the Hummelshain forest district with explicit approach (each left bar) and stratified approach (each right bar).

results to the coupled model TreeGrOSS-C allowed the projection of forest carbon stocks based on forest inventory that is routinely compiled in Central Germany. The model explicitly accounts for the mixed-species, multi-cohort stand characteristics. Studies on larger scales often stratify the forestry data and thereby abstract from details of stand structure. I studied if this stratification introduces a bias in projections of the ecosystem carbon sink by applying the TreeGrOSS-C model to 1616 plots the Hummelshein forest district by two approaches. In the first approach, I used all available data including all stands and cohorts. In the second approach I stratified the data according to species groups, age classes, and site classes and simulated each stratum with a single cohort. I found that at stand scale ecosystem carbon stocks and the carbon sink over 100 years calculated with the aggregated approach differed from the explicit approach (39% to +38% and -1.1 to +1.9 tC/ha/yr respectively), mainly because of the properties of the interspersed species. However, these differences were of opposing sign and compensated for each other across the forest district (Fig. 13). This effect of compensating effects at larger scales corresponds to the findings of Davi et al. (2006), who studied the effect on environmental parameters of a process based forest growth model. It implies that decisions on management for specific stands need proper information on stand structure. Conversely, it implies that the stratified approach is justified at larger scales. Further, the results confirmed that the age distribution of the studied area has a large effect on the projected carbon sink (Vetter et al. 2005, Albani et al. 2006, Böttcher 2007, Canadell et al. 2007).

7. Conclusions

The integration of several methodological developments and component models into the coupled model TreeGrOSS-C allowed the projection of the forest carbon sink of individual stands in Central Germany based on available data sources and routinely compiled forest inventories.

The presented developments include

- the integration of site inventory and forest inventory data (Publication I),
- the adaptation and validation of an empirical forest growth model to the conditions of a routine, standard forest inventory and management planning, specified for the federal state Thuringia (Central Germany),
- the development and integration of carbon quantification methods, which are based on forest inventory and harvest data, into the stand growth model (Publication II),
- the integration of a stand growth model, a management model, a wood product model, and a soil carbon model to a multi-cohort forest ecosystem carbon accounting model,
- the modelling of average past mean litter production and the investigation of the uncertainty of the results and their sensitivity to model parameters (Publication III)
- and, the development of the transient correction for initial soil carbon stocks regarding to former disturbance of soil carbon stocks (Publication IV).

The fact that the model can be applied to standard forestry data, made it possible to simulate the carbon sink of each individual stand of entire forest areas. By comparing the model application to a forest district in Central Germany with a stratified approach, I collected some evidence that multi-cohort and multi-species stand properties have an impact on ecosystem carbon stocks and fluxes at stand level but that their influence is levelled off at forest district scale (Publication V).

8. Future research

The implications of both, the changes in forestry management and the changing environmental conditions with global change for the forest carbon budget must be accessed at operational scale. In order to develop the presented approach further, two points need to be addressed. First, a more detailed specification and quantification of rules or new management practices is required

(Gamborg and Larsen 2003, Larsen and Nielsen 2007), in order to develop a more realistic management plan. Second, changing environmental conditions need to be more explicitly represented in the stand growth component model (Matala et al. 2006). Then, model experiments, which check the sensitivity to management and environmental conditions, combined with inventory data would allow to factor out several anthropogenic and natural effects on forest carbon stocks.

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Spatially Explicit Assessment of Carbon Stocks of a Managed Forest Area in Eastern Germany

Abstract The Kyoto-protocol permits the accounting of changes in forest carbon stocks due to forestry. Therefore, forest owners are interested in a reproducible quantification of carbon stocks at the level of forest management units and the impact of management to these stocks or their changes. We calculated the carbon stocks in tree biomass and the organic layer including their uncertainties for several forest management units (Tharandt forest, Eastern Germany, 5500 ha) spatially explicit at the scale of individual stands by using standard forest data sources. Additionally, soil carbon stocks along a catena were quantified. Finally, carbon stocks of spruce and beech dominated stands were compared and effects of thinning intensity and site conditions were assessed. We combined forest inventory and data of site conditions by using the spatial unions of the shapes (i.e., polygons) in the stand map and the site map. Area weighted means of carbon (C) stocks reached 10.0 kg/m² in tree biomass, 3.0 kg/m² in the organic layer and 7.3 kg/m² in mineral soil. Spatially explicit error propagation yielded a precision of the relative error of carbon stocks at the total studied area of 1% for tree biomass, 45% for the organic layer, and 20% for mineral soil. Mature beech dominated stands at the Tharandt forest had higher tree biomass carbon stocks (13.4 kg/m²) and lower organic layer carbon stocks (1.8 kg/m²) compared to stands dominated by spruce (11.6 kg/m²; 3.0 kg/m²). The difference of tree biomass stocks was mainly due to differences in thinning intensity. The additional effect of site conditions on tree carbon stocks was very small. We conclude that the spatially explicit combination of stand scale inventory data with data on site conditions is suited to quantify carbon stocks in tree biomass and organic layer at operational scale.

Keywords ecosystem carbon pools, temperate mixed spruce and beech forest, site conditions, thinning, forest management, spatial distribution, GIS, stand scale, landscape, error analysis

Introduction

Several studies quantify carbon stocks in forests by using national inventories for forests and soils (e.g. Baritz and Strich 2000, Dieter and Elsasser 2002, Karjalainen et al. 2002, Laitat et al. 2000, e.g. Liski et al. 2002, Schlamadinger 2003). Lindner et al. (2002) and Nabuurs et al. (2002) estimated carbon stocks in forests by usage of frequency distributions of forest types. All of these studies calculate carbon stocks and their errors accurately using statistics at the scale of nations or federal states, which is sufficient for the national communications to the UNFCCC (United Nations Framework Convention on Climate Change) (UNFCCC 1997). However, forest owners are interested in carbon pools at stand level and the level of forest management units. The above studies cannot account for the spatial heterogeneity of carbon stocks caused by different site conditions and forest management at this spatial resolution. Further, the development of methodologies for spatially explicit estimations based on inventories can support validation of long-term eddy-covariance measurements of carbon dioxide exchange above forests. As found at the flux tower site in the Tharandt forest, the total source area (ca. 1 km^2) contributing to the atmospheric fluxes of carbon dioxide comprises a series of individually managed forest stands (Bernhofer 2003).

The present study aimed (1) to quantify spatially distributed carbon stocks and their uncertainties in tree biomass, the organic layer, and mineral soil at stand scale for an entire forest management unit, and (2) to explore relationships between carbon stocks and dominating tree species as well as influences of thinning intensity and site conditions. Using the Tharandt forest in eastern Germany as a case study, it is demonstrated in how far standard forest inventory data are suitable for the quantification of carbon stocks, and how the spatial distribution can be used to relate differences in these stocks to different species, thinning activities and site conditions.

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Methods

Study Site

The Tharandt forest is located in Germany at 51° latitude and 13° longitude at elevations of 400 to 460m asl, about 20 km southwest of the city of Dresden. Mean annual air temperature is 7.2°C and mean annual precipitation is 800 mm (Bernhofer 2002). Most stands are dominated by Norway spruce (*Picea abies* [L.]. Karst.) interspersed with Scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), and European beech (*Fagus sylvatica* L.).

There are also several stands that are dominated by the latter species. While most of the younger stands include mixtures of different species, older stands are more homogenous.

The parent material is dominated by gneiss and porphyry. However it is very heterogeneous and partly covered by loess (Fiedler et al. 1989a). Dominant soil type is dystric cambisol. Podzols and stagnosols are also frequent. The forest area of 5500 ha comprised almost four forest management units. It was managed by the smallstrip-clearcutting system, which was commonly used in the former German Democratic Republic.

Data Sources

Forestry administration of the former German Democratic Republic performed an inventory of forest biomass for each stand every ten years. The inventory provides information of the area of the stands [m²] and tree parameters of homogeneous groups of trees within each stand: species, age [year], quadratic mean of diameter at breast height (DBH) [cm], height [m] (calculated from stand height curve for given DBH), timber volume [m³/ha], and basal area [m²/ha]. The inventory does not contain the variance of tree parameters, timber volume of trees with a DBH smaller than 7cm, nor the number of trees within a group of trees. We used an inventory of Tharandt forest that was conducted in 1988 and the last amendment by yield tables was done in 1993. The link between records of forest inventory and the location in space is provided by the stand map. Each shape (i.e., polygon) of the stand map refers to an administratively formed area that consisted of one or a few stands.

During 1960 – 1970, forestry administrations of the Eastern Germany started an inventory of site conditions (Kopp and Schwaneke 1991). The raw data of the soil profiles have been aggregated and classified to site classes. A site class consists of the categorical site parameters of climate/topography, parent material, water regime, nutrient availability, and moisture index. The parameter parent material, in this inventory, is a mixed description of topography, soil type, and bedrock. Moisture conditions are described by the two parameters water regime and moisture index. Water regime describes the seasonality of moisture (alternating: clear seasonality, constant: no change with time, variable: other wetness-specific classes e.g., moisture dynamics near well-springs). Moisture index defines ordinal subclasses of water availability within each class of water regime. Local experts delineated areas of homogeneous site parameters using mainly topography and vegetation. Results of this survey are provided in the site map. Each shape of the site map has a site class and a local classification of soil types assigned to it. Details on the site parameters and their categorical values can be found in the literature (Gemballa et al. 2001, Rehfuess 1990, Schwaneke 1989, 1965). In this paper we try to use terms of the world reference base soil classification (WRB) (FAO 2006) where possible, despite there is no unique mapping between WRB and the soil classification of this inventory.

Additionally, we used data of 10 soil profiles out of a transect (the Esberg Catena, Fiedler et al. 1989b) for quantifying mineral soil carbon stocks. Profiles were taken from soil pits, which extended down to bedrock and were analysed according to German soil classification (AG BODEN 1994). Locations of the soil profiles comprised different soil types. For each mineral horizon (Pietrusky 1975) and (Fiedler et al. 1989a) measured coarse stone content and carbon content. We further determined fine soil bulk density per mineral horizon by using a mixed sample of fife soil cores (100 cm^3).

Combining the Data Sources

Data on site conditions were related to shapes of the site map while records in the forest inventory were related to shapes of the stand map. However, stand map and site map did not match. In order to combine the maps and their related records we used an approach that was based on the spatial **union of maps** via a GIS (Figure 1).

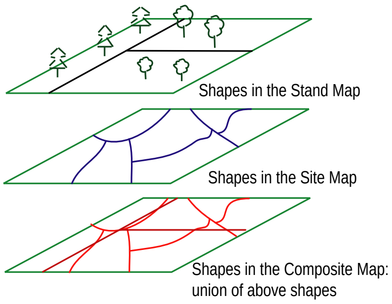

Figure 1: Union of the shapes of the stand and site map. Each shape of the composite map corresponds to exactly one shape of the stand map and one shape of the site map.

We used the information system `CQuant` (Wutzler 2002) to relate information from both, forest inventory and site parameters to the corresponding shapes of the united map. For each shape of the united map carbon stocks were quantified using the combined dataset. As far as not mentioned otherwise, units of calculated masses refer to pure carbon (e.g., kg/m^2). Finally, the results were aggregated to the corresponding shapes of the stand map or the site map by an area-weighted mean (equation 1). Several shapes of the composite map correspond to one stand of the stand map or one site class in the site map.

$$\bar{c}_K = \frac{\sum_{i \in K} A_i \cdot c_i}{\sum_{i \in K} A_i} \qquad (1)$$

where $\bar{c}_K$: mean result of area K (set of shapes) [kg/m²], i: index of the shapes within area K, A_i: area of shape i [m²], c_i: carbon stock per area for shape i [kg/m²]

Spatially Explicit Error Propagation

For estimating the relative error of the spatial mean, relative errors of the areas were assumed to be small compared to relative error of the carbon stock estimates. Hence, the size of areas can be considered to be exact. Further, we assumed carbon stocks to be uncorrelated between stands. With the rules of error propagation for uncorrelated sums and products, the relative error of the mean carbon stock from equation 1 is calculated by equation 2.

$$R(\bar{c}_K) = \frac{\sqrt{\sum_i \left(A_i \cdot c_i \cdot R(c_i)\right)^2}}{\sum_i (A_i \cdot c_i)} \qquad (2)$$

for area K [kg/kg], i: index of the shapes within area K, A_i: area of shape i [m²], c_i: carbon stock per area for the shape i [kg/m²], $R(c_i)$: relative error of carbon stock for shape i [kg/kg]

Similarly, stocks and errors can be aggregated to other coarser spatial levels e.g., the entire study site, or all area that is dominated by a specific species.

Tree Biomass Carbon Stock Quantification

We calculated the **biomass** of each tree homogenous tree group by using biomass expansion factors (BEF) according to equation 3.

$$m_{CTreeGroup} = V * D_R * BEF * C_{conc} \qquad (3)$$

where $m_{CTreeGroup}$: carbon stock of the tree group [kg]; V: timber volume [m³ dry wood including bark]; D_R: wood density [kg/m³], BEF biomass expansion factor [kg/kg]; C_{Conc}: carbon concentration [kg/kg]

For spruce the BEFs of Wirth et al. (Wirth et al. 2004) were used (Table 1). They are dependent on age and site index. For pine the age dependent combined factors (KBEF = D_R * BEF) of Lehtonen et al. (Lehtonen et al. 2004) were applied. For pine we used a higher uncertainty than reported, because the factors were developed in Finish forests. For other coniferous species, the BEF of spruce were applied, but densities as reported by Löwe et al. (2000) were used. For beech Wirth et al. (2004) report age-dependent combined factors. All other broadleaved species were treated like beech but corrected for wood density (density of species / density of beech). We used species-specific carbon contents that were reported by Weiss et al. (2000).

For estimating the relative error of a tree group carbon stock, we can assume the errors of timber volume, density, BEF, and carbon content to be independent. Hence, relative error equals the sum of squared relative errors of the single factors.

Table 1: Factors for estimating tree carbon stocks. (a): (Wirth et al. 2004) (b): (Lehtonen et al. 2004), DR: dry wood density, C_{Conc}: carbon concentration, BEF: biomass expansion factor, KBEF: D_r*BEF

Species	**D_R [kg/m³] (Löwe et al. 2000)**	**C_{Conc} [%] (Weiss et al. 2000)**	**BEF [kg/kg]**
spruce	377 (a)	50.1	(a) Site index >34 = 1.544 + 0.999 * exp(-0.094 * age); Site index < 25 = 1.89 + 2.41 * exp(-0.085 * age) medium site index: = 1.655 + 2.366 * exp(-0.114 * age)
pine	430	51.1 (like fir)	(b) KBEF = 0.7018 + 0.0058 * exp(-0.01*age)
beech	550	48.6	(a) KBEF = 0.74 + 0.636 * exp(-0.018 *age)
other coniferous	larch 430; others 370	51	like spruce
other broadleaved	oak: 560, others: 550	oak 49.5, locust 49.2, ash 49.7, cherry 49.7, birch 48.5, others 49	like beech

Table 2: Relative errors (R) for estimating stand tree carbon stocks. (a) (Wirth et al. 2004) (b) (Weiss et al. 2000) (c) (Lehtonen et al. 2004), R(timber volume) = 12% (Kurth et al. 1994). DR, CConc,BEF, KBEF see table 1.

Species	$R(D_R)$	$R(C_{Conc})$	R(BEF)	Resulting $R(C_{Stock})$
spruce	9% (a)	1%	site index > 25: 5.6% (a) site index <= 25: 10% (a)	16.0% 18.1%
pine	11% (b)	1%	R(KBEF) = 6% ((c): reported 2.8%)	13.5%
beech	6% (a)	1%	R(KE) = 13.4%; R(KBEF) = 13.36%	18.0%
other coniferous	11% (b)	2%	site index > 25: 8% site index <= 25: 12%	18.2% 20.3%
other broadleaved	11% (b)	2%	15%	19.3%

Timber volume has a relative error (standard deviation / mean ≈ ¼ range of 95% confidence interval) up to 12% (Kurth et al. 1994). By using species-specific carbon contents we can assume relative errors to be below 1% for main species and below 2% for other species (Table 2). Table 2 also reports species-specific stand to stand density errors and errors of the biomass expansion factors. For combining the errors of all tree groups within one stand, independent errors of the tree groups are assumed and absolute errors are added.

Organic Layer Carbon Stock Quantification

Carbon stocks in the organic layer were estimated by regression models that have been developed for Thuringian forests. The models have been fitted to carbon stocks of O_l, O_f, and O_h layers that were measured at 178 plots in Thuringian forests (Wirth et al. 2004). According to the combination of bedrock and the dominating tree species one out of four models was selected. We checked applicability for the Tharandt forest at four spruce dominated stands where stocks were measured. In all models the single predictor was nutrient availability. The parameters bedrock and nutrient availability were derived from the data of the site evaluation in the following way. The categorical indices of site parameter nutrient availability was transformed to an ordinal scale (k, r (rich) →1; m (medium) →2; z, a (poor) →3).

The broad range of site parameter parent material was grouped and related to the required classification of bedrock (Table 3).

For each plot the relative prediction error of the regression model was assigned corresponding to the combination of species and bedrock (Wirth et al. 2004). Values range from 23% for conifers on soils dominated by loess to 73% for broadleaved forests on any parent material. In order to propagate the error of organic layer carbon stocks from the shapes in the united map to the stand, we divided the area weighted standard deviations (= stock · relative error) by the area weighted mean stock (equation 1).

Mineral Soil Carbon Stock Quantification

Calculation of **mineral soil** carbon stocks was based on a simple model of several homogenous layers (equation 4).

$$m_{CHorizon} = \Delta h \cdot (1 - r_{stones}) \cdot \sigma_{bulk} \cdot r_C \qquad (4)$$

$m_{CHorizon}$ carbon within pedogenetic horizon [kg/m²]

Δh height of the layer [m]

r_{stones} content of stones (d > 2mm) within soil volume [m³/m³]

σ_{bulk} fine soil (d < 2mm) bulk density [kg/m³]

r_C carbon content of fine soil [kg/kg]

We used pedogenetic horizons instead of fixed depths, because there are rapid changes in soil properties at the edge of horizons in stagnosols and podzols. These soil types comprise large parts of the study area. In order to compare soil types and site classes, the soil carbon stocks of soil horizons were summed over horizons within surface soil (A), subsurface soil (B) and soil influenced mainly by bedrock (C) (AG BODEN 1994).

The relative error can be calculated by equation 5 if factors are considered independent of each other.

$$R(m_{Horizon}) = \sqrt{\begin{array}{l} R(\Delta h)^2 + R(r_{stones})^2 \\ + R(\sigma_{bulk})^2 + R(r_C)^2 \end{array}} \qquad (5)$$

where R(x): relative error of factor x; other symbols as in equation 4. Δh: height of the layer

Table 3: Grouping of site parameter parent material.

hydro (L)	dominated by water regime (mainly gleysols and stagnosols) (site map indices Lg,Sg,B,Lu,Gg,Gu)
acidic (G)	dominated by acidic bedrock (Sf, P)
sand (S)	dominated by sandy bedrock (Sn, Sb)
loess (LL)	dominated by loess bedrock (LL,Ls,Lb,Gn)
basic (C)	dominated by basic bedrock (Ba)

Symbols in brackets in the first column represent the category identifiers that are used to select the regression model of organic layer carbon stocks (Wirth et al. 2004). Symbols in brackets at the second column represent identifiers of parent material according to the site evaluation (Schwaneke 1989, 1965).

[m], r_{stones}: content of stones (d > 2mm) within soil volume [m³/m³], σ_{bulk}: fine soil (d < 2mm) bulk density [kg/m³], r_C: carbon content of fine soil [kg/kg]

Ståhl et al. (2004) assumed relative errors of 30% fine soil bulk density, 40% stone content, 80% carbon content for a large scale inventory in Sweden. However, horizontal changes of stone content, layer thickness and likely also fine soil bulk density and carbon content are well captured by the stand map, which delineates changes across a few 10' m. Therefore, we assumed lower relative errors of 10% layer thickness, 20% stone content, 50% carbon content, and 15% fine soil bulk density within one horizon at the extend of a shape in the site map of fixed size. Assuming uncorrelated errors, standard error propagation (equation 5) resulted in a relative error (precisions) of a single horizon of 57%. We did not have estimates of correlations among the factors and the soil horizons. Inclusion of these correlations would decrease the relative error. Assuming independent errors of the horizons, the relative error at plot scale was calculated by equation 6. Relative error decreased with the number of sampled horizons per site.

$$R(m_{Plot}) = \frac{\sqrt{\sum_i \left(m_i \cdot R(m_i)\right)^2}}{\sum_i m_i} \tag{6}$$

where $R(m_{Plot})$: relative error of soil carbon stock at Plot (area of a site shape) [kg/kg]; i: index of soil horiozon; h_i: depth of horizon [m]; m_i: horzion carbon stock [kg]; $R(m_i)$: relative error of horizon carbon stock [kg/kg]

Raw data of mineral soil carbon stocks was sampled only for spruce dominated stands. We assumed no differences in mineral soil carbon stocks by dominating species, because these differences are small compared to differences with site conditions (Mund and Schulze 2005).

Statistical Analysis of the Species Effect on Tree Carbon Stocks

Information on tree groups in the inventory was available only for a part of the area of about 4080 ha. The other part consisted of non-stocked areas or very young stands, for which timber volume was not recorded in the inventory. The spatial distribution of carbon pools and the mean values refer to the stocked area only. Effects of species were studied using a constrained population. Stands dominated by age classes above 150 years (48.0 ha) were neglected, because extrapolating stocking density far from given yield table values is error-prone. Further, the **standtype constrained population** consisted of more or less monospecific stands related to the stand map (Figure 1, top). Mixed stands were excluded by requiring the dominant tree group to cover at least 65% of the stand's basal area and 65% of the stand area. This population covered 38% of the totally stocked forest area and 49% of the forest area that was dominated by spruce, pine, or beech. The same inventory record on different site conditions only counts as one entity in this population.

Significance of differences between carbon stocks of trees and the organic layer between spruce and beech was tested with an unpaired t-test. Area weighted means and their relative errors were calculated by equations 1 and 2, and variance of the mean values by equation 7. Next, the t statistics (Quinn and Keough 2002, p37) was calculated by equation 8. Finally, the probability of this statistics was obtained by the density distribution with n_{Beech} + n_{Spruce} - 2 degrees of freedom using the dt function of the R-statistics package version 2.1.1.

$$\mathrm{var}(\overline{m}) = \left(\overline{m} \cdot R(\overline{m})\right)^2 \tag{7}$$

where var($\overline{m}$): variance of area weighted mean carbon stock; $\overline{m}$: area weighted mean of carbon stocks; $R(\overline{m})$ relative error of area weighted mean carbon stock

$$t = \frac{\overline{m}_{Beech} - \overline{m}_{Spruce}}{\sqrt{\mathrm{var}(\overline{m}_{Beech}) + \mathrm{var}(\overline{m}_{Spruce})}} \tag{8}$$

where t : t-statistics applied for difference in stocks of beech and spruce. (Square of the standard error corresponds to the variance of the mean)

When studying effects on tree biomass carbon stocks, the number of observations was set to the number of observed stands. When studying effects on the organic layer, the number of observations was set to the number of plots that had been used to construct the regression models (beech 17, coniferous 160) (Wirth et al. 2004).

Statistical Analysis of Thinning Intensity Effect on Tree Carbon Stocks

In order to compare tree biomass carbon stocks by species across different thinning intensities we **corrected observed carbon stocks** of different thinning intensities to a comparable standard value. We used the proportion of actual basal area to the standard basal area (Kramer and Akça 1995) as a simple parameter of thinning intensity. In the following we refer to this proportion as **stocking density**. We interpolated standard basal area for each inventoried group of trees by using yield tables (Table 4), observed stand age, and interpolated site index. Site index was interpolated using yield tables, observed age, and height. Hence, standard basal area represents the expected (according to permanent study sites) basal area, and is dependent on site quality. If stocking density is smaller than one, stands have been thinned more intense than usual.

Correction was done in the following way. First, we fitted the equation "CBiomass = b_0 + b_1·ln(Age) + b_2·stockingDensity^2 + b_3·ln(Age):stockingDensity" for each species to the standtype-constrained population. Second, this models was used to predict carbon stocks with observed thinning intensity and stocks with thinning intensity 1 for each plot. Finally, each tree biomass carbon stock was corrected by the factor "predicted stock with standard thinning intensity / predicted stock with observed thinning intensity". Significance of the difference between mean corrected carbon stocks of beech and spruce was tested by an unpaired t-test (equation 7 and 8).

Statistical Analysis of Site Condition Effect on Tree Carbon Stocks

Not only thinning intensity, but also different site conditions potentially confound the effect of species on tree carbon stocks. In order to study the effect of site conditions the combined information of the site map and the stand map was used. The **site condition constrained population** that consisted of plots of the composite map (Figure 1, bottom) which had to comprise an area of at least 0.4 ha. In addition to the constraints for monospecific stands, we excluded plots on steep terrain (indicated by a flag in site map) and plots outside the main local climate class. Hence, precipitation, temperature and insulation were about the same in all studied plots. The site constrained population covered 33% of the totally stocked forest area and 41% of the forest area that was dominated by spruce, pine and beech. Plots with the same inventory record but different site conditions were treated as different entities.

Similar to correcting for different thinning intensities, we used regression models to correct additionally for the effects of nutrient availability, water regime, and moisture index. We experimented with many model forms (also including parent material) and investigated variance, residuals, and the Akaike Information Criterion (Akaike 1987). However, there was no clear favourite model. We present results, that were obtained with the following model: "CBiomass ~ ln(Age) + stockingDensity^2 + NutrientAvailability + WaterRegime + WaterRegime :MoistureIndex". The model equation contained coefficients and dummy variable for each level of the categorical factors (Quinn and Keough 2002, p136). The site parameter moisture was not treated as main effect because it describes subclasses of site parameter water regime.

Table 4: Yield tables used to interpolate stocking densities. Data from (Nicke 1997).

tree group	yield table
beech	Dittmar et al. (1986)
spruce	Wenk et al. (1985)
pine	Lembcke et al. (1976)
larch	Schober R (1987)

First, this model was fitted to the site condition constrained population for each species. Second, this model was used to predict carbon stocks with observed conditions and stocks with the fixed conditions (stocking density 1, medium nutrient availability, and moderate moisture of constant water regime) for each plot. Finally, each tree biomass carbon stock was corrected by the factor "predicted stock with fixed conditions / predicted stock with observed conditions". Significance of the difference between mean corrected carbon stocks of beech and spruce was again tested by an unpaired t-test (equation 7 and 8).

Results

Mean Carbon Stocks

Area weighted mean carbon stocks in above ground **tree biomass** amounted to 10.0 ±0.6 kg/m^2 (Figure 2 left, Table 5). This mean stock refers to the area, for which timber volume was recorded in the inventory (88% of total area). Related to total area, which includes also non-stocked areas and very young stands, mean carbon pool reached 8.8 kg/m^2. Largest carbon stocks of 22.5 kg/m^2 were found in stands dominated by old beech. Mean carbon stocks of the **organic layer** amounted to 3.0 ±1.35 kg/m^2. Maximum carbon stocks in the organic layer of 5.1 kg/m^2 were calculated for coniferous stands at sites with poor nutrient supply, while minimum organic layer carbon stocks of 0.8 kg/m^2 were calculated for deciduous stands at rich site conditions. In **mineral soil,** area-weighted carbon stock of the area around the transect was 7.3±1.4 kg/m^2. The relative carbon content in individual layers of the soil profiles is shown in Table 6. Each profile corresponds to a

Table 5: Mean carbon stocks in forest compartments of stands in the Tharandt forest.

	all	spruce	pine	beech
mean age [y]	73	82	78	87
tree biomass				
stock [kg/m²]	10.0	11.6	9.9	13.4
sd [kg/m²]	0.1	0.1	0.2	0.8
cv [%]	1%	1%	2%	6%
n	1228	375	80	20
organic layer				
stock [kg/m²]	3.0	3.0	3.5	1.8
sd [kg/m²]	1.4	1.2	1.6	1.3
cv [%]	45%	42%	45%	73%
n	177	160	160	17
mineral soil				
stock [kg/m²]	7.3			
sd [kg/m²]	1.4			
cv [%]	20%			
n	10			
total				
stock [kg/m²]	20.3	21.8	20.7	22.5
sd [kg/m²]	2.0	1.9	2.1	2.1
cv [%]	10%	9%	10%	9%

Mean values (stock), standard deviations (sd), coefficient of variation (cv) and number of samples (n) are indicated.

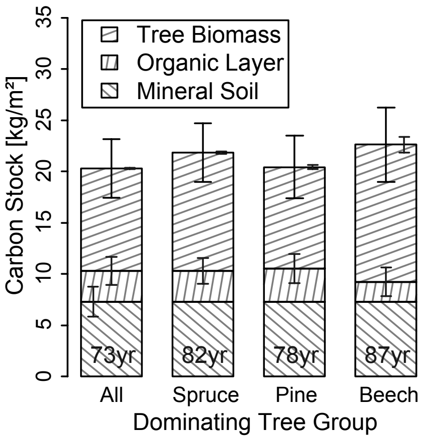

Figure 2: Area weighted mean main carbon stocks of stands in the Tharandt forest. Left bar represents all the entire stocked area including other species and mixed stands, the other three bars represent a constrained population of more or less monospecific stands. Arrows denote standard deviation of the area weighted mean stocks, numbers in the bars represent the area weighted mean age. For results of individual compartments see Table 5.

different site class. The maximum carbon stock 18.4 kg/m^2 was found at profile 18 (on loess dominated bedrock with a very deep A_{eh} horizon). The minimum carbon stock of 1.2 kg/m^2 was found at profile 24 (on acidic parent material with a thin A_{eh} horizon).

Table 6: Soil characteristics of individual horizons of the profiles studied at the Tharandt forest.

Pro-file	horizon	depth (cm) from	to	density (g/cm³)	Stones (%)	carbor (%)
1	arAh	0	5	0.6	0	5.2
1	aBv-Go	5	15	0.9	0	3.2
1	aGo-M	15	30	1.3	0	3.2
1	aGr	30	70	1.6	40	0.8
15	Aeh	0	5	0.9	5	5
15	Bsv	5	35	1.3	15	1.8
15	Bv	35	95	1.4	90	0
24	Ahe	0	8	0.5	0	2.75
24	AhBv	8	35	1.2	0	0
24	Bv-Sg	35	75	1.6	0	0
27	Ahe	0	6	0.8	50	6
27	Bv1	6	70	0.8	90	1.8
2	Aeh	0	4	1.1	5	2.1
2	Ae	4	20	1.5	8	0.3
2	Bsh	20	35	1.5	15	1.8
2	Bs2	35	110	1.5	5	0
5	Aeh	0	20	0.7	5	4.6
5	Bvs	20	50	1.3	15	3.5
18	Aeh	0	15	0.6	5	13.8
18	Ae	15	65	1.5	15	1
3	Ah	0	10	0.7	0	5.18
3	Ah-Sw	10	25	1.1	10	0
3	Sw	25	70	1.6	10	0
7	Aeh	0	10	1.1	15	12.4
7	Bv	10	25	1.3	20	0
23	Ahe	0	5	1.0	3	12
23	Bv-Sw1	5	65	1.4	20	0
23	Sw2	65	90	1.8	15	0

Profile numbers and Carbon content refer to Fiedler et al. (1989c) and Pietrusky (1975), horizon: description of soil horizons (AS Arbeitskreis Standortskartierung 1980).

Spatial Distribution of Carbon Stocks

The spatial distribution of carbon stocks in **tree biomass and the organic layer** is shown for a selected area southwest of the hill “Esberg” in the Tharandt forest as an example (Figure 3). We depicted this area, because it overlaps with the soil transect and there is a beech-dominated stand in the centre, which is of equal age as the spruce dominated stand right next to it. Similar patterns of species composition and age class structure are found across the total Tharandt forest. The spatial pattern of the distribution of carbon stocks in tree biomass followed the stand map, because it represents species composition and age class structure. The carbon stock of the spruce stands at the upper right increased with stand age. However, the beech dominated stand at the centre had a

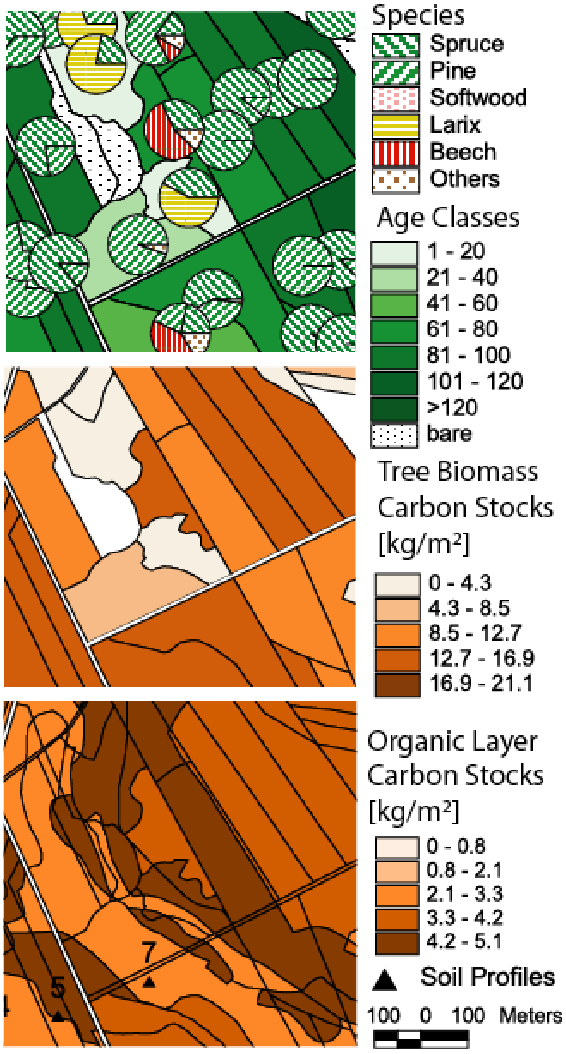

Figure 3: Spatial distribution of tree biomass and organic layer carbon stocks of several stands southwest of the hill "Esberg" in the Tharandt forest. Top) stand map showing species distribution and stand age (of the dominant tree group). Centre) tree biomass carbon stocks distributed according to the stand map. Bottom) organic layer carbon stocks distributed according to the composite map (union of the shapes of the stand map and the site map).

higher stock than the neighbouring spruce stand of the same age. On the other hand, the beech dominated stand had a lower organic layer carbon stock. Spatial distribution of calculated organic layer carbon stocks, additionally, showed a pattern that followed the site map which has curvy edges, because different bedrocks are represented by this map. Spatial distribution of **mineral soil** carbon stocks showed a pattern that was related to the relative position to the slope (Figure 4). Plots with highest pools were all located at the slopes or near the bottom of the slopes. Low stocks were found at the plateau and lowest stocks are at the more level terrain of the surrounding area with shallow soils. There was a large range of values within a small distance.

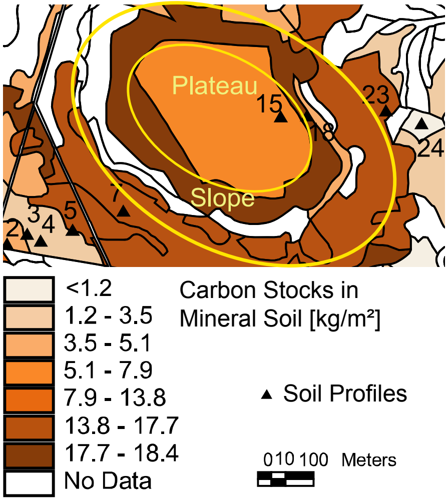

Figure 4: Spatial distribution of mineral soil carbon stocks across and around the hill "Esberg" distributed according to the site map. Triangles mark the location of the soil profiles for mineral soil carbon stock quantification. Labels represent soil profiles numbers.

Different Carbon Stocks of Spruce and Beech dominated Stands

Beech dominated stands had a significantly higher (1.83 kg/m², p=0.026) mean tree carbon stock than spruce dominated stands. This difference is not due to the slightly higher mean age of beech stands compared to spruce and pine, because beech stands have higher stocks in each age class (Figure 5 top). Contrary, there was also a non-significant trend of lower carbon pools in the organic layer (-1.05 kg/m², p=0.34) of beech dominated stands (Figure 6) with all parent materials except the ones, which were dominated by water (label hydro, mostly gleysols and stagnosols). With assuming neglectable differences in soil carbon stocks between species, total carbon stocks of beech dominated stands had a weak trend to slightly higher stocks (0.77 kg/m², p=0.4) than spruce or pine dominated stands (Figure 2, Table 5).

Effect of Thinning Intensity and Site Conditions on Carbon Stocks

Beech dominated stands are located at more favorable site conditions and are managed with higher stocking densities than the other stands (Figure 7). Correcting the stocks for the effect of stocking density yielded a decrease in beech carbon stocks at ages 50 to 110 years and an increase in coniferous carbon stocks (Figure 5 center). At these age classes, spruce dominated stands had slightly higher corrected carbon stocks than beech dominated stands. The difference between area weighted means (Equation 1) of corrected tree carbon stocks of beech and spruce

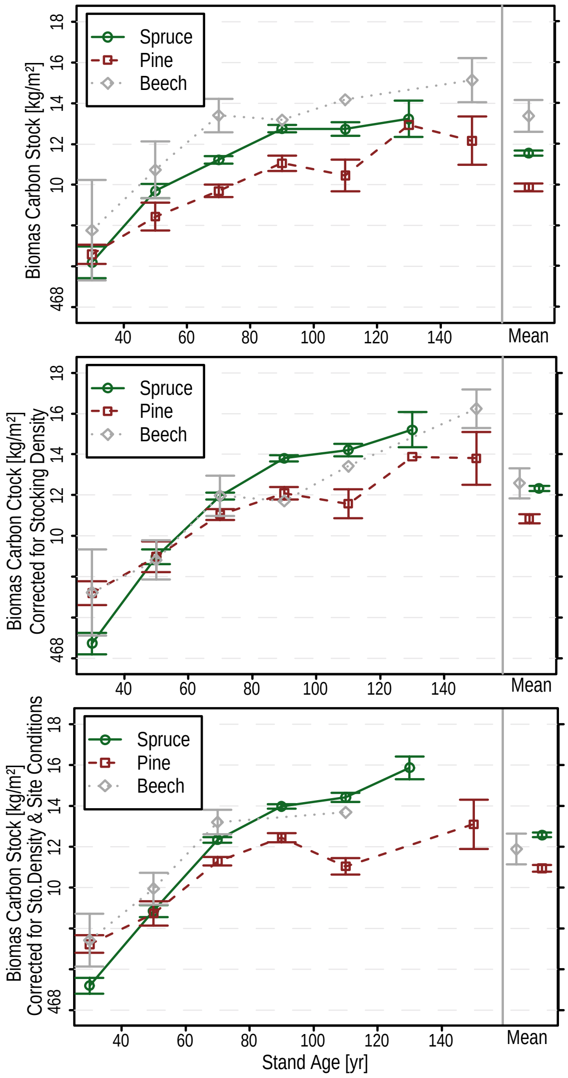

Figure 5: Area weighted mean tree biomass carbon stocks by species and age classes (21-40, 41-60, …). Arrows denote standard deviation of the area weighted means. Top) observed stocks. Centre) stocks corrected for stocking density by a regression model; Bottom) stocks corrected for stocking density, nutrient availability and moisture conditions.

decreased to 0.26 kg/m². This difference was not significant any more (p=0.38).

Correcting additionally for site conditions had only a marginal effect on tree carbon stocks (Figure 5 bottom). The drop of mean carbon stock of beech in the last correction is explained by the exclusion of many old beech stands at very steep sites when constructing the site constrained population. The differences in mean age in the site constricted population (beech 60yr, spruce 82yr) resulted in a lower area weighted mean tree carbon stocks of beech compared to spruce (-0.69 kg/m², p=0.26).

Organic layer carbon stocks were clearly influenced by site conditions, i.e., the parent material (Figure 6) and nutrient availability.

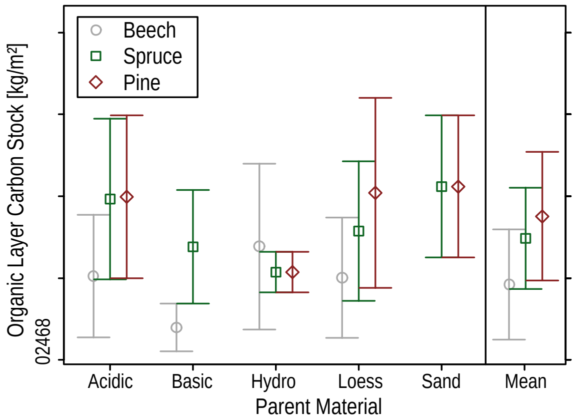

Figure 6: Organic layer carbon stocks by species and parent material. Mean values are area weighted. Error bars denote area averaged standard deviation.

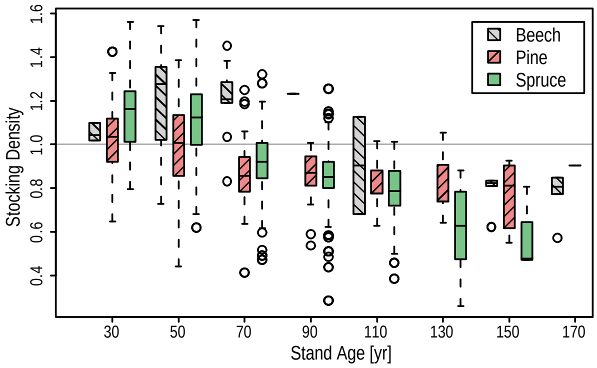

Figure 7: Distribution of stocking densities at th Tharandt forest by age classes of (21-40, 41-60, …). I this case, stocking density is the proportion o inventoried basal area to basal area suggested by yiel tables (Table 4). It reflects thinning and harvestin strategies. Stands with values greater than 1 are thinne less than usual management, stand with values less tha 1 are thinned stronger. The usual boxplots display th distribution of the values by the median (center of th box), 25% and 75% percentiles (hinges), minimum an maximum values (arrows), and outliers i.e. value greater than 1.5 times the spread outside the closes hinge (circles).

Within the sparse dataset of the mineral soil there was no specific single site parameter that had a clear influence with mineral soil carbon stocks (Figure 8). However, there were similar mineral soil carbon stocks with the same combination of site conditions (profile numbers 24 and 27, numbers 18 and 5).

Discussion

The most important aspect of this study is the **spatially explicit quantification** of carbon stocks at the scale of a forest management unit in Central Europe at the resolution of individual forest stands based on standard forestry data. The spatially explicit results enable combined analysis with other spatial data sources. In this study we used

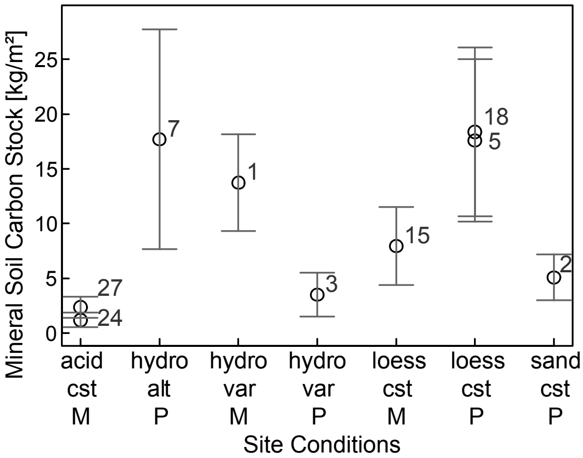

Figure 8: Mineral soil carbon stocks of the soil profiles by combination of site parameters. acidic, hydro, loess, sand: different parent materials (see Table 3); cst, var, alt: water regimes of different seasonality of moisture (constant, variable, alternating); M,P: moderate and poor nutrient availability. Error bars denote standard deviation of the calculated stock (equation 5 and 6).

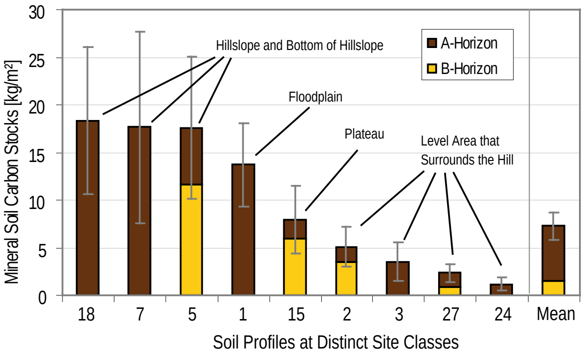

Figure 9: Mineral soil carbon stocks by profiles ordered descending. Mean values are area weighted. Error bars denote standard deviation of the calculated stock (equation 5 and 6). Labels indicate the position relative to the slope.

the spatial combination of data of forest inventory and data of the site evaluation. This allowed the quantification of organic layer carbon stocks at stand scale (Figure 3, bottom) and it allowed the comparison of influences of stand characteristics and site conditions on tree carbon stocks (Figure 9). Other applications with e.g., digital elevation data or results of ground water modelling become possible but go beyond the scope of this paper. We spatially combined the stand and site datasets using the union of the shapes (Figure 1). In contrast, Wolff (2002) combined the stand and site datasets at grid points and regionalized results on the basis of regions with similar growth conditions. The approach of this study has the advantage of allowing the analysis of several carbon pools at the same high spatial detail. However, it is scalable only to the federal states of Germany that perform a stand based forest inventory. The focus on spatial distribution at this scale is new to carbon inventories in Central Europe. Hence we know only of one similar study from Thuringia (Wirth et al. 2004) and one study from France (Le Maire et al. 2005), which spatially quantifies carbon fluxes.

Results of the mean **tree biomass carbon stocks** in the Tharandt forest (8.8 kg/m² in relation to total forest area) agree with results from studies in Thuringia of 8.2 kg/m² (Wirth et al. 2004) and a German management case study (8.7 kg/m²) (Karjalainen et al. 2002). They were lower than national inventory (9.8 kg/m²) (Baritz and Strich 2000). This is because there are higher stocks in the southern parts of Germany. Observed stocking density was low (Figure 7). This was likely due to extensive thinning during novel forest decline before the inventory in 1988. Hence, carbon stocks will increase with increasing stocking density. There are considerable differences in biomass expansion factors. The use of recent factors that were dependent on stand age and site index increased mean carbon stocks by the number of 1.7 compared to the factors used by Baritz and Strich (2000) (coniferous 1.14; broadleaved 1.24) for the first German national reporting. **Carbon stocks of the organic layer** (3.0 kg/m² Table 5) agree with the national inventory (2.1 kg/m²) (Baritz and Strich 2000), and agree with the Thuringian study (2.7 kg/,²) (Wirth et al. 2004), because we utilized the same quantification algorithm which is based on differences between stand types, parent materials and nutrient availability. At four spruce dominated stands mean organic layer carbon stocks of 4.8 kg/m² have been measured (Persson, personal communication). At these plots the used model estimated organic layer carbon stocks to 3.9 kg/m². This underestimation of 18% is within the error range of 42% for spruce stands. Area-weighted mean of **mineral soil carbon stocks** (7.3 kg/m² Table 5) agree with estimates of soil carbon in Thuringia (7.0 kg/m²) (Wirth et al. 2004) and with the national inventory (8.8 kg/m²) (Baritz and Strich 2000). All the stands, in which soil profiles were located, were dominated by spruce. There are indications that species composition affect incorporation of organic matter into the mineral soil (Fischer et al. 2002). However, these effect vary with site conditions (Berger et al. 2002) and they are small compared to differences caused by site conditions (Mund and Schulze 2005).

In comparison to carbon quantification studies that used national inventories (e.g, Baritz and Strich 2000, Dieter and Elsasser 2002, Ståhl et al. 2004) we used **stand scale inventories**. These stand scale inventories comprise a larger number of samples per area but trade in a lower precision of the single timber stock measurement (12% relative error, Kurth et al. 1994). The errors are of the two inventory types are comparable only at the same scale. When aggregating several single measurements to a comparable scale, the variance of the mean stock reduces with the square root of the sample number (Weiss et al. 2000). This is also true for the area explicit error propagation (equation 2). With the individual stand approach also the bias due to correlation between BEF and timber volume shown by Vilén et al. (2005) for sample inventories is bypassed. At the total stocked area of the Tharandt forest the relative error of the mean carbon stock in tree biomass was only 1% (Table 5). However, the different estimates for biomass expansion factors that were reported (Levy et al. 2004) suggest, that there might be a bias when applying the factors apart from the region, where the factors were assessed. Further, there might be also a bias in the stand scale timber volume measurement. The bias does not decrease with the number of measured plots.

A similar reasoning is true for mineral soil carbons stock errors based on **sampling stratified for site classes**. We could use only a low sample size of 10 plots, however, in comparison there are only 4 plots of the national soil inventory (BML 1996) at the total Tharandt forest. The approach of this study has the advantage of explicitly stratifying for more or less homogenous areas of mineral soil carbon stocks (Figure 4). The relative error of mineral soil carbons stocks at plot scale is dominated by the real heterogeneity of the stocks within the plot, and only to a part by measurement errors. Therefore we can justify choosing lower estimates of relative error of the measured factors compared to Ståhl et al. (2004), whose single plots represented a vastly greater area. Usage of the small scale inventory was the precondition of the spatial union and the comparison of influencing factors at the scale of forest management units.

When analyzing the **factors that influence carbon stocks**, we found a significant influence of site conditions only on organic layer carbon stocks (Figure 6). Effects of site condition on tree biomass carbon stocks were overshadowed by effects of stocking density (Figure 5). This implies that forest carbon models that currently focus on environmental conditions ,e.g., Biome-BGC (Thornton 1998), should include thinning activities in a more explicit way. Further, we did not find relationships between single factors of site conditions and mineral soil carbons stocks (Figure 8). The large differences in mineral soil carbon stocks within short distances imply that extrapolation studies should aggregate the results of single plot measurements using the areas of a proper stratification, e.g. the shapes of the site map. The only factor that effected mineral soil carbon stock that we noticed, was the position relative to the slope in the catena (Figure 4). This can be seen more clearly when arranging the profiles by carbon stock (Figure 9). The only exception of high mineral soil carbons stock afar from the slope was profile 1 near the source of a little brook. We can not draw conclusions from this sparse dataset because there are many confounding factors (bedrock, ground water table, etc.). However, this spatial pattern could be related to horizontal transport processes. This would imply that models of soil carbon dynamics to take such processes into account. Further it would imply that extrapolation studies that are based on large-scale inventories could stratify plots by small-scale topography. This topic needs further research.

The used approach of accounting for differences in stocking density and site conditions by using regression models (Figure 5) is only valid if there are not too many differing factors. We could ensure this by constraining the studied population to a not too large area of the same climate and similar topography. If the studied population encompasses larger area, there are too many confounding factors. However, it is necessary to account for different influencing factors as it was demonstrated in the comparison of tree biomass carbon stocks between species.

Beech dominated stands had higher tree biomass carbon stocks than stands dominated by spruce in the Tharandt forest (Figure 2, Table 5). This was a combined result of lower stand density of beech stands, a higher wood density of beech stem wood, and a slightly higher beech BEF (Table 1). This was not alone a species effect, but also an effect of different management. Stocking density was lower in spruce dominated stands (Figure 7) and accounting for this effect rendered the difference between theses species insignificant (Figure 5 center). At the time of the inventory forest management did not promote mixed species stands. However, there were many interspersed tree groups in younger stands that probably originated from natural regeneration. This observation enforces the need for research on mixed species stands. The results of comparing species are based on a much smaller population that excluded mixed stands in comparison to the results of the total forest that included all available stand data. We did not investigate shrubs and ground vegetation. However, these pools could contribute considerable carbon stocks, specifically at low stand densities (Solon and Roo-Zielinska 2003). With changes in forest management also dead wood can become important again in managed forests (BML 2004). An evaluation of species concerning carbon sequestration requires consideration of mean retention times of the wood products, changing growth conditions due to climate change and risks of disturbances. Considering only the main differences in current tree biomass stocks and organic layer stocks in the forest, we can recommend promoting beech in forests with similar site conditions as the Tharandt site.

This study focused on carbon stock quantification. The average stock is relevant for climate change mitigation, because the difference in carbon stocks is removed from the atmosphere carbon pool. For short term changes the **carbon dynamics** (i.e. fluxes and turnover) is more important. There are different effects of thinning intensity and site conditions on this factor, because with favourable site conditions carbon turnover is higher (both, increased uptake and increased respiration and export). In order to investigate dynamics, the inventory data has to be combined with modelling studies (Kurz et al. 2002). This will also give insight in underlying ecosystem processes. However, this is future work for Central European forests at this scale.

Conclusions

Standard forestry data was sufficient to quantify carbon stocks of tree biomass and the organic layer spatially explicit at stand scale. This was possible by combining data sets using the union of the stand map and the site map. Quantification of mineral soil carbon stocks required further soil sampling.

Usage of small scale inventories with a low precision at plot scale (18% of carbon stocks in stand tree biomass and 57% in mineral soil horizon) allowed a reasonable precision at the scale of forest management units (1% tree biomass carbon stocks and 20% mineral soil).

High small scale spatial heterogeneity implied the necessity to explicitly account for the areas represented by the single plots when aggregating to coarser scales.

The spatial combination of data sources allowed comparing different factors that influence carbons stocks. The accounting for confounding effects by regression models proofed to be a helpful tool at this scale. Thinning activities significantly affect tree biomass carbon pools. However, we did not find a significant affects of site conditions on tree biomass carbon pools within the same climate. Mature beech dominated stands at the Tharandt forest had higher tree biomass carbon stocks and lower organic layer carbon stocks compared to spruce. This was to a big part an effect of differences in thinning intensity.

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Generic biomass functions for Common beech (*Fagus sylvatica L.*) in Central Europe – predictions and components of uncertainty

Abstract This study provides a comprehensive set of functions for predicting biomass for Common beech (Fagus sylvatica L.) in Central Europe for all major tree compartments. The equations are based on data of stem, branch, timber, brushwood (wood with diameter below 5 or 7 cm), foliage, root and total above-ground biomass of 443 trees from 13 studies. We used non-linear mixed-effects models to assess the contribution of fixed effects (tree dimensions, site descriptors), random effects (grouping according to studies) and residual variance to the total variance and to obtain realistic estimates of uncertainty of biomass on aggregated level. Candidate models differed in their basic form, the description of the variance, and inclusion of various combinations of additional fixed and random effects and were compared by the AIC criterion. Model performance increased most when accounting for between-study-differences in the variability of biomass predictions. Further, performance increased with the inclusion of age, site index, and altitude as predictor variables. We show that neglecting variance partitioning and the fact that prediction errors of trees are not independent with respect to their predictor variables will lead to a significant underestimation of prediction variance.

Keywords inventory, allometric equation, regression, mixed-effects models, upscaling, covariance, stem, branch, timber, foliage, root, brushwood

Introduction

The estimation of biomass at the tree-level and the subsequent step of scaling up biomass to the stand and eventually the regional level using forest inventory data is an essential component of monitoring carbon storage in forests (Kauppi et al. 1992, Liski et al. 2006, Nabuurs et al. 2003). Advances in the quality and the efficiency of carbon monitoring will affect decisions on climate politics and energy politics (Raupach et al. 2005). Furthermore, accurate forest carbon stocks are important to validate models (Thurig and Schelhaas 2006, Vanclay and Skovsgaard 1997) and for validating spatial extrapolations based on

List of Symbols

Symbol	Unit	Description
symbols of tree measure and predictors		
m	kg	biomass
d	cm	diameter at breast height (1.3m)
h	m	tree height
age	yr	tree age
si	m	site index (mean height of trees at age 100 years)
alt	m	altitude (height above sea level)
dh		models with predictors diameter and height only
dhc		models with additional covariates *age*, *si*, and *alt*
statistical symbols		
i		group (study)
j,k		individuals (trees)
y_{ij}		target variable (biomass m)
x_{ij}		vector of predictors. (d,h)
v_{ij}		vector of covariates (age,si,alt)
β		vector of fixed effects
b_i		vector of random effects
c_s		coefficients c_0, c_1, and c_2 of the basic model forms
int		intercept (constant)
ε		residual
σ^2		variance or first coefficient of the variance model
δ		second coefficient of the variance model

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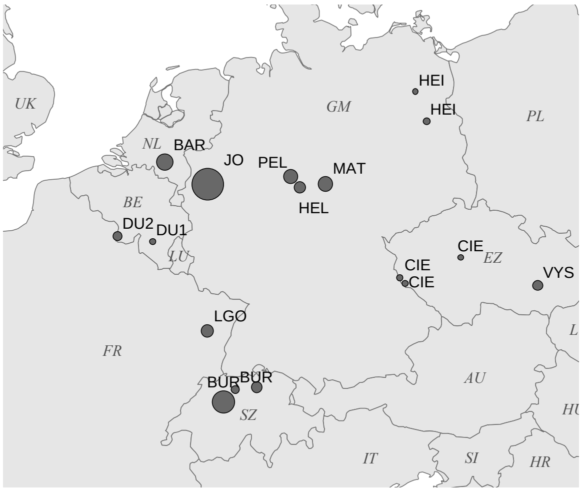

Figure 1: Map showing the location of study sites. The plot labels correspond to the studies listed in Table 1. The size of the symbols increases with the number of trees sampled at the location.

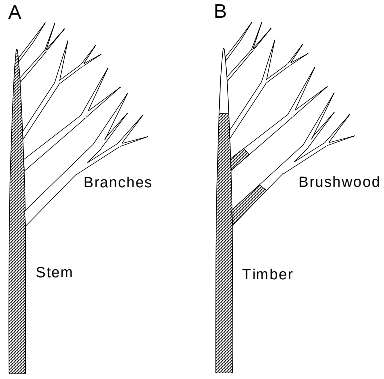

Figure 2: Schemes of different definitions of above ground woody biomass compartments. Scheme A separates between stem and branch wood with the assumption that the main stem can be clearly identified all the way to the top. Scheme B which is less subjective and most commonly applied in forest sciences separates between timber and brushwood based on a fixed diameter threshold (usually 5 or 7 cm).

remote sensing (Lu 2006). The basis for the assessment of forest carbon stocks are biomass equations. These equations relate variables that are commonly measured during forest inventories, such as tree diameter at breast height, to dry mass of biomass compartments. They may be applied directly at the tree level, or as a component of biomass expansion factors, which operate on aggregated data at the stand-level (Jalkanen et al. 2005, Wirth et al. 2004a).

There are numerous studies on biomass equations of different species for different regions (Jenkins et al. 2003, Marklund 1987, Zianis et al. 2005) and also several studies for common beech (Table 1) (Hochbichler 2002, Hochbichler et al. 1994, Lebaube et al. 2000, Zianis and Mencuccini 2003, 2005). With the exception of Burger (1949/50) and Joosten et al. (2004) the biomass equations presented in these studies are limited with respect to the number of trees (median 20 trees, minimum 7 and maximum 38 trees), the size range of the sample trees, and the extent of the study area (mostly single stands or catchments). None of these studies is sufficiently representative for a nationwide monitoring of forest carbon stocks and covers a large enough environmental gradients to be applicable to such a large and diverse area as Central Europe. Furthermore, none of the above studies provides the statistical background information to allow a straightforward variance estimation of stand- and regional level biomass (for other species see Phillips et al. 2000, Wirth et al. 2004b). Nor, can this information be provided by meta-analysis-studies that are based on published equations instead of tree measurements (Muukkonen 2007, Zianis and Mencuccini 2003). However, uncertainties of biomass predictions are as important as the predictions themselves (e.g. Raupach et al. 2005). And finally, most studies only report data and equations for a subset of the biomass compartments. Compartments considered usually include the economically relevant above-ground woody compartments (timber, stem), less often branches and leaves and rarely belowground compartments. However, monitoring and modelling changes of carbon stocks requires the estimation of all the biomass compartments.

In our study we compiled available biomass data for Common beech (*Fagus sylvatica* L.) and developed generic biomass equations applicable for a broad range of sites and situations and for all major biomass compartments. In addition, we provide tools for a realistic estimation of uncertainties of biomass predictions that account for the heterogeneity of the underlying data. We used non-linear mixed-effects models in order to make inference on variance components. We outline how functions of biomass and functions of prediction variance were developed and how they can be used to estimate variances and confidence intervals for individual tree predictions as well as for estimates of biomass stocks on aggregated-level, e.g. stands, from forest inventory data. While the aggregation of stand-level predictions and uncertainties to the regional level involves further steps, our generic equations for the wide-spread Common beech – covering 15% of the forest area in Germany – will serve as an important component in an improved national carbon monitoring.

Methods

Data

We collected biomass of tree compartments from sample trees of Common beech originating from 13 studies (Table 1), which cover the extent of Central Europe quite well (Fig. 1). The tree-level entries included biomass *m* of a tree compartment (kg) and as predictor variables the diameter at breast height *d* (cm), the tree height *h* (m), and the

Table 1: Methods used and compartments sampled by 13 studies to determine tree biomass of Common beech.

ID	Study	n_{Tree}[a]	n_{Plot}	Country[b]	Compartments[c]	Altitude [m]	Site Index [m]	Variables[d]	Comments
BAR	(Bartelink 1997)	38	6	NL	agr,st,br,l	23	34 - 36	sr,cl,cp	
BUR	(Burger 1949)	91	18	SZ	bw,l	480 - 1360	24.5 - 36	sr	br included thin stem parts and was not considered here
CIE	(Cienciala et al. 2006)	20	4	EZ	agr,st,br	450 - 750	24 - 28	cl,cp	
DU1	(Duvigneaud et al. 1971)	7	1	BE	agr,st,br,t,bw	330	26		reconstructed tree heights
DU2	(Duvigneaud et al. 1977)	13	1	BE	agr,st,br	250 - 250	24	cl	
HEI	(Krauß and Heinsdorf 1996)	14	3	GM	agr,st,br,l	42	28.5 - 30		also quantified bark
HEL	(Heller and Göttsche 1986)	29	3	GM	agr,t,bw,r	500	22.5 - 24	sr	r only for 4 trees
JO	(Joosten et al. 2004)	116	28	GM	agr,t,bw	30 - 500	18 - 45.5		
LGO	(Le Goff et al. 2004)	23	2	FR	agr,st,br,l,r	300	36	sr,cl	r only for a subset
MAS	Masci, A. pers. comm. within project FORCAST (Schulze et al. 2003)	28	1	IT	agr,st,br,l,r	1560	18	sr,cl,cd	r only for a subset
MAT	Matteucci, G. pers. comm. within project FORCAST (Schulze et al. 2003)	30	3	GM	agr,st,br,l	440 - 450	32 - 35		l only for a subset
PEL	(Pellinen 1986)	19	5	GM	agr,t,bw,l,r	420	29 - 30.5	sr	r only for a subset, age uncertain
VYS	(Vyskot 1990)	15	1	EZ	agr,st,br,l,r	505	36	sr,cl,cd,cp	also quantified twigs and stump, provides further data on root
	Total	443	76	7		23 - 1560	18 - 45.5		

[a] n_{Tree} = number of sample trees considered; n_{Plot} = number of plots where trees have been samples;

[b] NL = Netherlands, SZ = Switzerland, EZ = Czech Republik, BE = Belgium, GM = Germany, FR = France, IT = Italy

[c] agr = above ground wood; st = stem including bark; br = branches; t = timber (agr with diameter > 7cm); bw = brushwood (agr with diameter < 7cm); l = leaves, r = roots

[d] in addition to diameter at breast height, tree height, age, site index and altitude: sr = social rank, cl = crown length, cd = crown diameter, cp = crown projection

Table 2: Number of sample trees and range of predictors by tree compartments.

Compartment	nTree	nStudy	Dbh (cm)	Height (m)	Age (yr)	Site Index (m)	Altitude (m)
agr	350	12	1 - 79	2 - 37	8 - 173	18 - 46	23 - 1560
stem	187	9	2 - 79	3 - 37	8 - 165	18 - 36	23 - 1560
branches	175	8	2 - 64	3 - 37	8 - 165	18 - 36	23 - 1560
timber	170	4	1 - 79	2 - 35	18 - 173	18 - 46	30 - 500
brushwood	276	6	1 - 79	2 - 40	14 - 173	18 - 46	30 - 1360
root	48	5	3 - 38	7 - 29	21 - 160	18 - 36	300 - 1560
leaves	247	8	1 - 62	3 - 40	8 - 165	18 - 36	23 - 1560

tree age *age* (yr). Stand-level predictors are the site index *si* (mean height of trees at age 100 years in m) and the altitude *alt* (height above sea level in m).

The biomass compartments considered are foliage (*leaves*), coarse roots (*root*) and above-ground woody biomass (*agr*). Due to the weak apical dominance of Common beech there is a gradual transition between stem and branch wood, which renders the separation into these two compartments ambiguous (Fig. 2). In this study we report functions for both schemes and thus for all four compartments: brushwood, timber, stem, and branches. The number of sample trees and the range of predictor values differed between compartments (Table 2).

Basic model forms

We used three basic model forms as starting points of our model selection. First, the simplest allometric equation for predicting the biomass of a tree compartment *m* is a function of its diameter at breast height *d* (eq. 1). It can be shown that the functional form of a power function arises from the assumption that the ratio of the relative growth rates of mass and diameter (here *m* and *d*) is constant (Wenk et al. 1990). Second, to improve the predictive power this basic allometric equation is often extended to include the tree height *h* as an additional predictor. Eq. 2 still can be viewed as allometric equation that relates biomass to the volume of a cylinder defined by *d* and *h* (Cienciala et al. 2006, Wirth et al. 2004b). Third, a multiple allometric equation for predicting the biomass of a tree compartment as a multiplicative function of *d* and *h* is given by eq. 3 (Widlowski et al. 2003).

[1] $m = c_0 d^{c_1}$ (d2)

[2] $m = c_0 \left(d^2 h\right)^{c_1}$ (dh2)

[3] $m = c_0 d^{c_1} h^{c_2}$ (dh3)

Here m is the biomass of a tree compartment for a sample tree, d is the diameter at breast height (cm), h is the tree height (m), c_s, i.e. $c_0..c_2$, are model coefficients to be estimated. The number at the end of the equation labels (d2, dh2, dh3) indicates the number of parameters.

Rational of using nonlinear mixed-effects models

We used non-linear mixed-effects models (Lindstrom and Bates 1990) to directly fit the candidate models to the data. The main advantage of using mixed-effects models lies in their capability to account for groupings in residual variance due to random effects (Pinheiro and Bates 2000). In our case, the grouping variable is the study from which the data originate. The mere fact that sample trees from one study usually share a common provenance and were collected in the same environment by the same team of scientists with a specific set of methods often causes their residuals to be consistently lower or higher than the mean predictions of a fixed effects model. This violates a fundamental assumption of independent residuals in conventional regression analysis (Crawley 2002), and will lead to an underestimation of variance. Mixed-effect models are one way to adequately address this type of data heterogeneity. Instead of assuming the same fixed effects across all groups (eq. 4a), mixed models allow the coefficients c_s of the model (eq. 1..3) to vary between groups by adding a group dependent random effect (eq. 4b). Additionally, they allow to include covariates that in part explain the deviation from generic coefficient value β_s (eq. 4c).

[4a] $c_s = \beta_s$

[4b] $c_s = \beta_s + b_{s,i}$

[4c] $$c_s = \beta_s + b_{s,i} + \beta_{s,age} \cdot age + \beta_{s,si} \cdot si + \beta_{s,alt} \cdot alt + \beta_{s,age.alt} \cdot age \cdot alt + \beta_{s,si.alt} \cdot si \cdot alt$$

,where β_s and $\beta_{s,<\mathrm{cov}ar>}$ are fixed effects, $b_{s,i}$ is the study dependent random effect, *age*, site index (*si*), and altitude (*alt*) are covariates.

For a single level of grouping to studies, the tree compartment biomass m_{ij} of the tree *j* from the i^{th} study can be expressed as the target by a single level mixed-effects model (eq. 5) (Lindstrom and Bates 1990)

$$[5] \qquad m_{ij} = y_{ij} = f\left(x_{ij}, v_{ij}; \beta, b_i\right) + \varepsilon_{ij}$$

$$b_i \sim N(0, \Psi), \text{ and } \varepsilon_{ij} \sim N(0, \sigma^2)$$

where, f is a general, real-valued, differentiable function (one of eq. 1..3, with coefficients expressed as eq. 4c) of a vector of predictors, x_{ij} (*d, h*), a covariate vector v_{ij} (*age, si, alt*), the vector of fixed effects β, and study dependent vector of random effects b_i (Pinheiro and Bates 2000). In this study we used an unconstrained symmetric positive definite covariance matrix Ψ of random effects. We used extended mixed-effects models, where the assumption of the within-group residuals $\varepsilon_i = (\varepsilon_{i1}, ..., \varepsilon_{in})$ is relaxed by $\varepsilon_i \sim N(0, \sigma^2 \Lambda_i)$, and where Λ_i are positive-definite matrices parameterized by a set of parameters δ_i. Typically the variance of the residuals ε_j increases with compartment biomass m_j for tree j at the original scale. We thus explicitly modeled the variance of the residuals by a power function (eq. 6).

$$[6] \qquad Var(\varepsilon_j) = g\left(\varepsilon_j; \sigma^2, \delta\right) = \sigma^2 \left|m_j\right|^{2\delta}$$

Not only the coefficients but also the residual variance may potentially vary between studies. We accounted for this by modifying the model of residual variance (eq. 6) to eq. 7 by replacing the single exponent δ by the group-dependent exponent δ_i.

$$[7] \qquad Var(\varepsilon_{ij}) = g\left(m_{ij}; \sigma^2, \delta_i\right) = \sigma^2 \cdot \left|m_{ij}\right|^{2\delta_i}$$

for the i^{th} study and the j^{th} observation. The parameters σ^2 and δ_i were estimated by iteratively re-weighted sum of squares simultaneously with the other coefficients in the model fitting algorithm.

We used non-linear models (Lindstrom and Bates 1990) for the following reasons. For model fitting the biometric data are often log-transformed to linearize the allometric equation and to homogenize the variance, which otherwise increases with size on the original scale (Baskerville 1972). However, the back-transformation of the predicted value to the original scale introduces biases in the expected values and the uncertainties (Smith 1993). The proper dealing with these biases introduces new assumptions and the simple nonparametric correction using the smearing estimate (Duan 1983, Taylor 1986), as it is frequently employed (e.g. Joosten et al. 2004), is not directly applicable if mixed-effects models are used (Wirth et al. 2004b). In addition, the logarithmic form does not allow to include the covariances between predictions errors at the original scale when calculating the variance of a biomass prediction errors for several trees (eq. A2.1). In Appendix A2 we show how the variance of new predictions can be propagated to aggregated levels.

Fixed effects models partition the variance around the mean prediction into the variance arising from uncertainty in the parameter estimates and into residual variance. In mixed-effects models a further component is added: the variance that is induced by the random effects, which represents groupings in the data (eq. A1.2)

In our case the random effect accounts for all implicit differences between sites, provenances and methods etc. associated with the sample material and sites of different studies that are not represented by any specific predictors. Besides the grouping of variances according to studies there is potentially also a grouping according to stands. In addition to the presented results we tried to fit two-level mixed models to account for this additional grouping level. However, the highly unbalanced design of the data, i.e. several studies include only one stand, and the differences in variances of random effects between the studies caused problems in the numerical algorithm to fit the two-level mixed model and we concluded that the available data was not sufficient to account for groupings at both the stand- and the study-level at the same time. Diagnostic graphs of stand level random effects and study level random effects showed that groupings according to studies were much more pronounced than groupings according to stands. In the presented approach the stand-level differences are partly accounted for by the study random effect. This approach can be seen as a pooling of the comparatively similar stands of each study in order to obtain enough within-group cases.

It shall be noted that the equations for the different compartments are based on different subsets of the whole dataset. Hence, we separately fitted the models for the different biomass compartments and the derived biomass equations are not additive (Lambert et al. 2005, Parresol 2001).

Definition of the candidate model set

In order to find an appropriate model, we compared 246 models for each biomass compartment by the Akaike information criterion (AIC) (Akaike 1987). Figure 3 summarizes the

- d2,dh2,dh3: basic model forms (eqs. 1..3)
- ran: inclusion of study random effects in model coefficients ($b_s = b_{s,\text{int}} + b_{s,i}$)
- c: inclusion of covariates in model coefficients (eq. 4)
- ranres: inclusion of a study effect in the residual model (eq. 7 instead of eq. 6)

Figure 3 Dimensions of the candidate model set.

different dimension of constructing the candidate model set.

First, we tested which coefficients (c_s) differed randomly by study. We fitted the models (eqs. 1..3) with all 8 combinations of random effects (either eq. 4a or eq. 4b) for the model coefficients and compared model performance by AIC. The non-linear fixed or mixed-effects model after this step is called the 'best dh-model'. In some cases with random effects in three or two coefficients the model fitting algorithm did not converge. We excluded these cases from the candidate model set.

Second, we included covariates in the model coefficients (eq. 4c). To reduce the number of possible combinations and to avoid overly complex models we constructed our candidate models according to the following three rules: (1) Higher-order polynomial terms for any of the covariates were avoided because such models are difficult to extrapolate. (2) A covariate effect was added to a coefficient c_s only if the same covariate effect was not already associated with another coefficient. This was done because including covariates on correlated coefficients caused unrealistically high counteracting effects (e.g. c_0 strongly increases with age while c_2 decreases with age). (3) Covariates were added to either c_1 or c_2 , in the dh3 model form (eq. 3) because diameter and height were highly correlated and the AIC hardly changed when the covariate was included in either one of the two coefficients. If the dh-model with random effects in c_0 and c_2 resulted in a better AIC than the dh-model with random effects in c_0 and c_1, we selected c_2 else c_1. In total, this led to 41 combinations of the terms in eq. 4 across the three coefficients. Finally, the resulting best model, which included the random effects from the first step, was compared to the models with covariates but with fewer random effects. We call the resulting best model after this step the 'best dhc-model'.

Third, we assessed if including a study dependent formulation of the residual variance increased model performance by replacing eq. 6 by eq. 7.

The model fitting was done using the nlme and the gnls functions using a general positive-definite variance-covariance matrix using Maximum Likelihood (ML) method for model selection. The resulting best models were refitted using the REML method to improve estimates for the variance components. We used R-nlme library version 3.1-66 (Pinheiro and Bates 2000).

Calculation of Confidence intervals

We computed symmetrical 95% confidence intervals around single tree biomass predictions with width $w_{cf95} = 2 \cdot 1.96 \cdot \sqrt{Var(m_{new})}$. The variances of the predictions were computed by eq. A1.2 and the residual variance component $Var(\varepsilon_{new})$ was determined by eq. A1.5. A numerical example for the tree-level calculation is given in Appendix A3.

At aggregated level the 95% confidence intervals around the biomass predictions were calculated with the same equation as for the tree level. However, the variance of the prediction error of the sum of the biomass of several trees has to include covariances between the single tree-level predictions errors (eq. A2.1 and eq. A2.3). The covariance between predictions errors of two trees explicitly depends on the predictors and covariates of the two trees (eq. A2.2). All calculations were programmed with the statistical software R[1]. The calculation of variance at the stand level was exemplified[2] using data of an inventory of a chronosequence of shelterwood beech forests in Thuringia, Germany (Mund 2004)[3].

Cross validation and comparison to previously published biomass functions

The validity of the presented model and its performance in comparison to published studies is demonstrated using cross validation (Davison and Hinkley 1997). This was done by comparing the predictive performance of a range of published

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[1] www.r-project.org. The programmed R-model objects, including variance-covariance matrices, derivative functions, and additional functions to apply prediction and uncertainty calculation at tree and stand level are provided as supplementary material S5

[2] R-code is provided with electronic supplementary material S6.

[3] Details of the inventory are provided with electronic supplementary material S1.

functions with the results of the cross-validation of our generic functions. In the cross validation the observations that were used for validation were not used to fit the model, i.e. the biomass of a tree from a given study was predicted with our generic model, but the parameterization of the respective model was based only on the data of all other published studies. For each model we calculated the root mean squared error (RMSE) with the modification of applying a weighted mean. The weights were the inverse of the square root of the expected variance according to eq. A1.5.

Results

Comparison of the models without additional covariates

The three-parameter model dh3 (eq. 3) fitted the data best for most compartments (see Table 3 for the example of stem biomass[4]). Only for the stem and timber biomass, the dh2-model (eq. 2) and for the root biomass the d2-model (eq. 1) showed similar or better performance. In all cases, the inclusion of parameters that allow the variance to differ between studies (eq. 7) resulted in the largest improvement of model performance. In comparison, the mere inclusion of random components into the model coefficients improved the model performance only slightly for the compartments stem, branches, roots, and leaves. However, it did not improve the model performance at all for the compartments above-ground wood and timber. The coefficients of the best dh-models are listed in Table 4.

Table 3: Comparison of the model forms and inclusion of random components by AIC for stem.

Kind of Model	AIC	degrees of freedom
dh3_c_ran_ranres	1507.3	17
dh2_c_ranres	1509.0	16
dh2_ran_ranres	1512.8	15
dh3_ranres	1538.3	13
dh3_c_ran	1567.2	9
dh3_ran	1571.3	8
dh2_c	1596.5	7
dh2	1623.6	4

dh3,dh2,d2: basic model forms (equations 2..4), c: covariates included, ^{c} ran: random effects included, ranres: model of residuals includes study dependence. results of the other compartments are given in electronic supplement S2 (Fig. 3)

Effect of additional covariates

The inclusion of the additional covariates age, site index, or altitude improved the model performance in all cases (see Table 3 for the example of stem biomass[5]). The highest improvement was achieved for the compartments above ground wood, branches, brushwood, and leaves (Fig 4; compare neighboring graphs). The coefficients of the best dhc-models are listed in Table 5. We will come back to the magnitude and sign of individual coefficients and their interpretation in the Discussion section.

Variance of predictions

The estimated parameters that are needed to calculate the residual variance (eq. A1.5) are listed in Table 6. The standard deviations of the random effects with the dhc-models in Table 6 were smaller compared to the ones of the corresponding dh-models. This indicates that a large part of the variance that was previously accounted for in the random effects component was now accounted for by the covariates.

The 95% confidence intervals of several single tree biomass predictions by the best dh-models (Table 4) and dhc-models (Table 5) are shown in Fig. 4. In all cases, the width of the confidence intervals strongly increased with the size of predicted biomass. This represented the increasing variability in the observed biomass that was modelled with a power model (eq. 6 or 7 respectively). The amount of prediction variance differed considerably between the different compartments. The confidence intervals for above ground wood biomass and timber are comparatively narrow (both have a coefficient of variation *cv* = 12% for tree age of about 70 years). However, confidence intervals of single tree biomass predictions of branches, root, and leaves are very wide (*cv* = 59%, 35%, and 49% respectively). The inclusion of additional covariates in the models resulted in narrower confidence intervals in most cases (compare neighbouring graphs in Fig. 4). However, the confidence intervals for branches and leaves were still comparatively wide (*cv* = 45% and 43%). Inclusion of additional covariates also accounted for a large part of the variance that, before, in the dh-models was attributed to unknown random effects between the studies (see background bars in Fig. 4).

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[4] For other compartments see electronic supplementary material S2

[5] For other compartments see electronic supplementary material S2

The biomass equations were developed at tree level. However many applications make inference at the aggregated level, e.g. stands, by taking the sum of predicted biomass of all trees. At the stand level, the confidence intervals were much narrower (Fig. 5) (cv = 2.5%, 2.9% for above ground wood and timber) compared to the corresponding confidence intervals at the tree

Table 4: Regression coefficients (β_i) and their standard errors in brackets of the best models of diameter and height (dh-models, eq. 1..3, with coefficients as in eq. 4b).

Compartment[a]	Form		β_0	β_1	β_2
agr	dh3	ranres	0.0523 (0.00330)	2.12 (0.0225)	agr
stem	dh2	ran_ranres	0.0293 (0.00406)	0.974 (0.0163)	stem
branches	dh3	ran_ranres	0.123 (0.0296)	3.09 (0.107)	branches
timber	dh3	ranres	0.00775 (0.00125)	2.11 (0.0406)	timber
brushwood	dh3	ran_ranres	0.466 (0.0862)	1.85 (0.100)	brushwood
root	d2	ran_ranres	0.0282 (0.00263)	2.39 (0.0467)	root
leaves	dh3	ran_ranres	0.0377 (0.00686)	2.43 (0.0817)	leaves

[a] This table is also available with electronic supplementary S2. Empty cells denote the term to be not included

Table 5: Regression coefficients and their standard errors for the models that include additional covariates (dhc-models, eq. 1..3, with coefficients as in eq. 4c).

Compartment	agr	stem	branches	timber	brushwood	root	leaves
Form	dh3 ran_ranres	dh3 ran_ranres	dh3 ran_ranres	dh2 ran_ranres	dh3 ranres	d2 ranres	dh3 ranres
β_0	0.0551 (0.00463)	0.00351 (0.00704)	0.122 (0.0294)	0.0106 (9.43E-04)	0.805 (0.159)	0.0292 (0.00225)	0.0561 (0.00882)
β_1	2.11 (0.0242)	1.84 (0.0333)	3.09 (0.106)	1.08 (0.00795)	1.83 (0.113)	1.70 (0.0792)	2.07 (0.0770)
β_2	0.589 (0.0427)	1.04 (0.0548)	-0.151 (0.304)		-0.560 (0.149)		-1.09 (0.112)
$\beta_{s,age}$	s=2: 4.06E-04 (1.07E-04)	s=0: 3.47E-05 (2.43E-05)			s=1: 0.00134 (3.03E-04)	s=0: 4.36E-05 (1.65E-05)	
$\beta_{s,si}$	s=0: 2.39E-04 (8.15E-05)	s=0: 6.72E-04 (2.38E-04)	s=2: -0.0309 (0.00783)			s=1: 0.0209 (0.00387)	s=1: 0.0137 (0.00192)
$\beta_{s,alt}$	s=0:-4.68E-06 (1.39E-06)	s=0: 8.11E-06 (2.77E-06)	s=2:-9.87E-04 (2.58E-04)	s=0:-1.54E-06 (5.84E-07)	s=1:-1.68E-04 (5.26E-05)	s=1: 7.43E-04 (1.72E-04)	s=0: -3.29E-06 (3.62E-06)
$\beta_{s,si.alt}$			s=2: 3.06E-05 (1.08E-05)			s=1:-2.70E-05 (8.55E-06)	

[a,] see Table 4, see appendix A3 for an example of constructing the full equation.

Table 6: Uncertainty coefficients of the best models.

	Compartment[a]	Form	σ^2 [b]	$Mean(\delta_i)$ [c]	$Var(\delta_i)$	$sd(b_{0,i})$ [d]	$sd(b_{1,i})$	$sd(b_{2,i})$
dh-models	agr	dh3	0.166	0.770	0.00965			
	stem	dh2	0.0708	0.873	0.0177	3.47E-07	0.0176	
	branches	dh3	0.249	0.863	0.0274			0.132
	timber	dh3	1.29	0.614	0.0104			
	brushwood	dh3	0.149	0.979	0.00448		0.0811	
	root	d2	0.0432	0.902	0.118		0.0660	
	leaves	dh3	0.179	0.854	0.117	0.00882		
dhc-models	agr	dh3	0.142	0.782	0.00912			
	stem	dh3	0.0903	0.842	0.0196	0.00316		
	branches	dh3	0.250	0.860	0.0260			0.0690
	timber	dh2	1.29	0.615	0.00779			
	brushwood	dh3	0.191	0.935	0.00434		0.0661	
	root	d2	0.0410	0.874	0.185			
	leaves	dh3	0.174	0.858	0.121			

[a] seeTable 4; The estimated covariance matrices of the fixed and the random effects are provided with electronic supplementary S4 in csv format, [b] σ: base variance [c] δ_i: power of variance for study *i*, [d] sd($b_{s,i}$): estimated standard deviation of the random coefficients

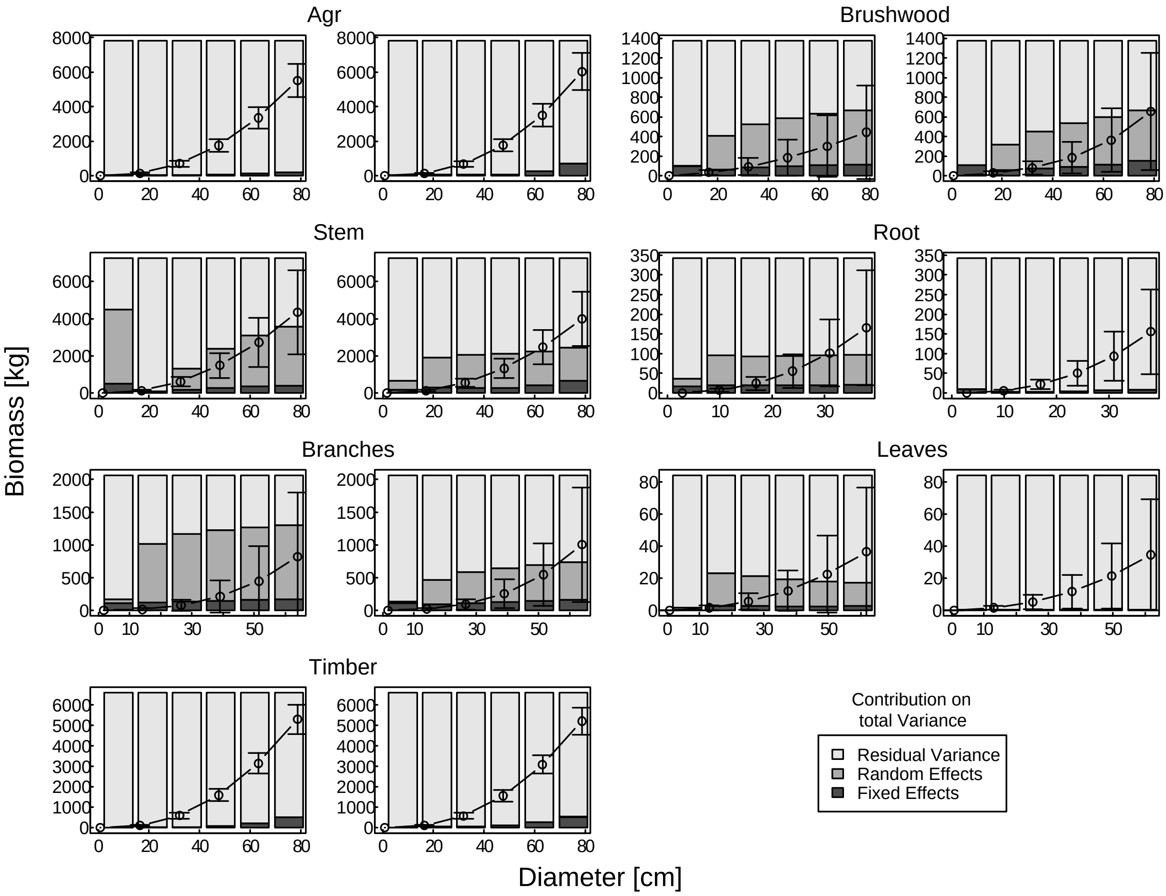

Figure 4 Tree-level predictions and 95% confidence intervals of the best dh-models (left) and dhc-models (right) for each biomass compartment, respectively. The bars in back represent the proportions of the different variance components (residual, random effects and fixed effects variance). The predictors site index and altitude were kept constant (*si* = 30m, *alt* = 470m). The predictors height and age were chosen to be consistent with the site index and the diameter.

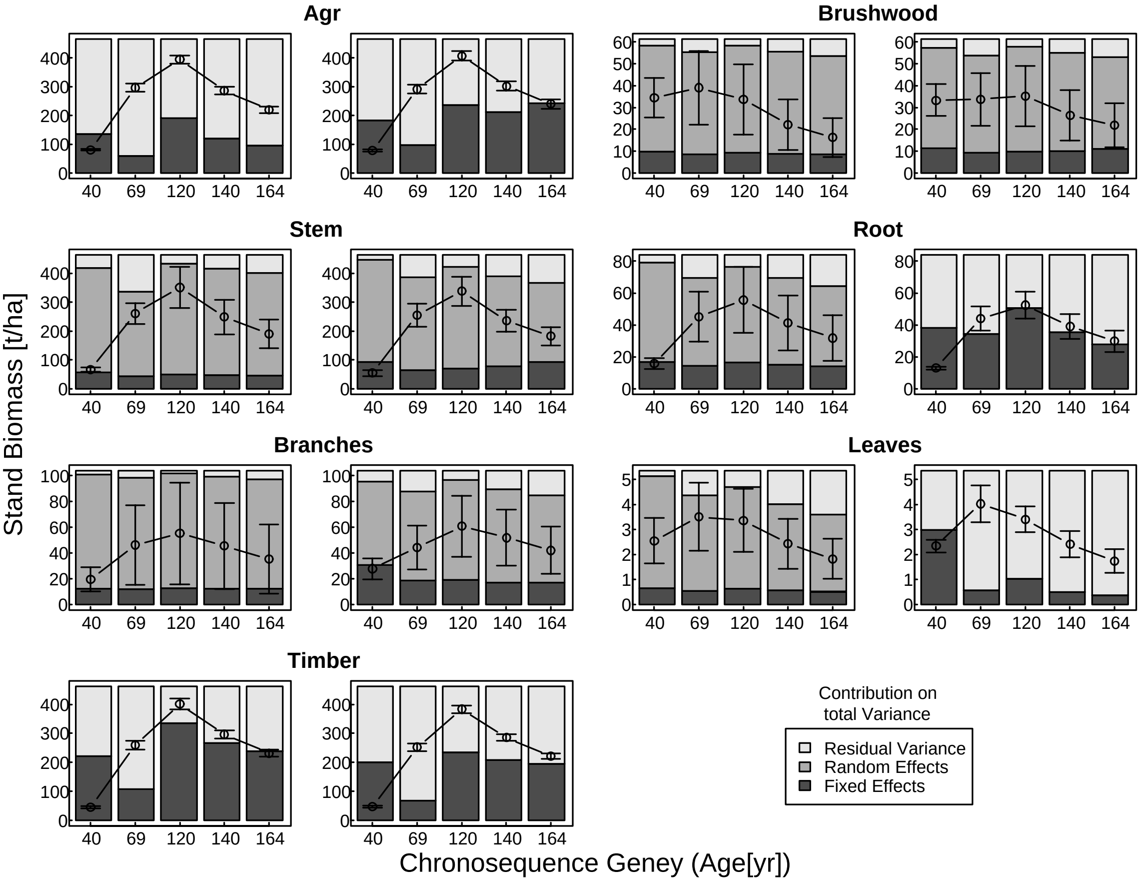

Figure 5: Predictions and 95% confidence intervals of the best dh-models on the left and the best dhc-models on the right for biomass predictions at the stand level for 5 stands of a shelterwood chronosequence. The bars in back represent the proportions of the different variance components as in Fig. 4.

level (Fig.4). The effect of wider confidence intervals for higher biomass predictions was still present, but not as pronounced as with the single tree biomass predictions. The relative contribution of model residuals to total variance was much smaller (background bars in Fig. 5). The decrease in total variance upon inclusion of covariates was much stronger than at the tree-level (cv = 34%→20%, 18%→8%, and 20%→10% for branches, root, and leaves, respectively, at stand age 69 years).

The different model forms are compared exemplarily for stem biomass at tree level in Fig. 6. The predictions were very similar for average covariate values. However, the variability between studies added uncertainty to the biomass prediction. The mixed-effects dh-model accounted for these differences by random effects, which resulted in a wider confidence band. The mixed-effects dhc-model explained these differences in part by additional covariates and the width of the confidence band was smaller than without covariates. The fixed effects model neglected the inter-group variability and underestimated the variance. Hence, the confidence band for the dh-fixed effects model was too narrow. However, this underestimation of variance due to ignoring differences between studies was small compared to ignoring covariances between single tree prediction errors at stand scale (Fig. 7).

Cross Validation

The advantages of generic models of the dh- and dhc-type can be evaluated by comparison with other published beech biomass functions for Central Europe that are based on far smaller data sets. The stem biomass predictions of the cross validation of the dh-models (including only diameter and height as predictors) were very similar to the predictions of the previously published equations by Ciencala et al. (2006) and Bartelink (1997) across the range of sizes (Fig. 8a). For our generic functions, the inclusion of additional covariates in the dhc-model improved the model fit slightly (weighted RMSE decreased from 21 to 18 kg). For foliage biomass, however, the larger dataset and the inclusion of covariates led to a more pronounced improvement of the model fit and a reduction of estimated biomass (Fig. 8b) in comparison to the predictions according to Bartelink (1997) and Le Goff and Ottorini (2001).

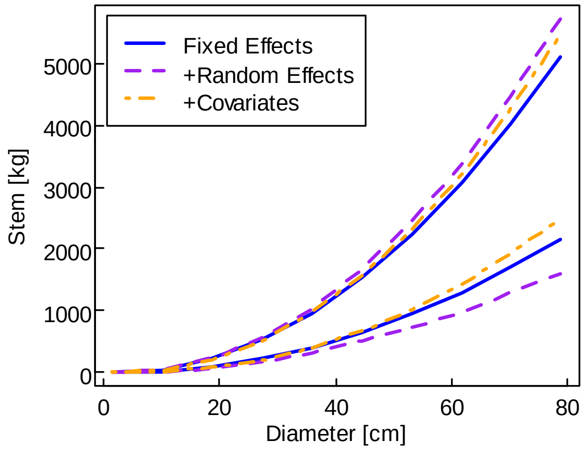

Figure 6: 95% confidence intervals of stem biomass for different forms of modelling variation between groups. Predictors site index and altitude were given intermediate values (*si* = 30m, *alt* = 470m). The predictors age, diameter and height were chosen to represent typical values for these conditions from the dataset of sample trees.

Discussion

Our study provides the first comprehensive set of functions for predicting biomass for Common beech in Central Europe for all major tree compartments. Combining original tree biomass data from many sites across Central Europe, which varied in climate and soil characteristics, it was possible to develop generic equations that are representative for the great majority of beech sites in the study region. However, the obvious advantages of combining data from various sources comes at the cost of data heterogeneity, which can only be appropriately dealt with by using non-standard statistical methods (Bates and Watts 1988, Wirth et al. 2004b). We used non-linear mixed-effects models (Pinheiro and Bates 2000) that have been successfully applied in forestry studies for trunk circumference (Lindstrom and Bates 1990), tree height (Calama and Montero 2004, Calegario et al. 2005, Fang and Bailey 2001, Hall and Bailey 2001), stand and bole volume (Fang et al. 2001, Gregoire and Schabenberger 1996, Zhao et al. 2005), yield (Hall

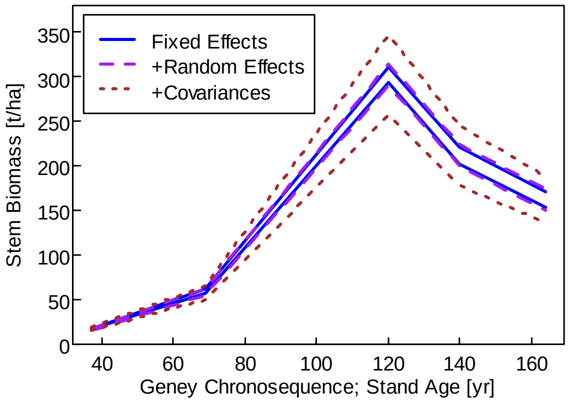

Figure 7 95% confidence bands of stem biomass at stands of the Geney beech forest chronosequence. None of the displayed model results used additional covariates.

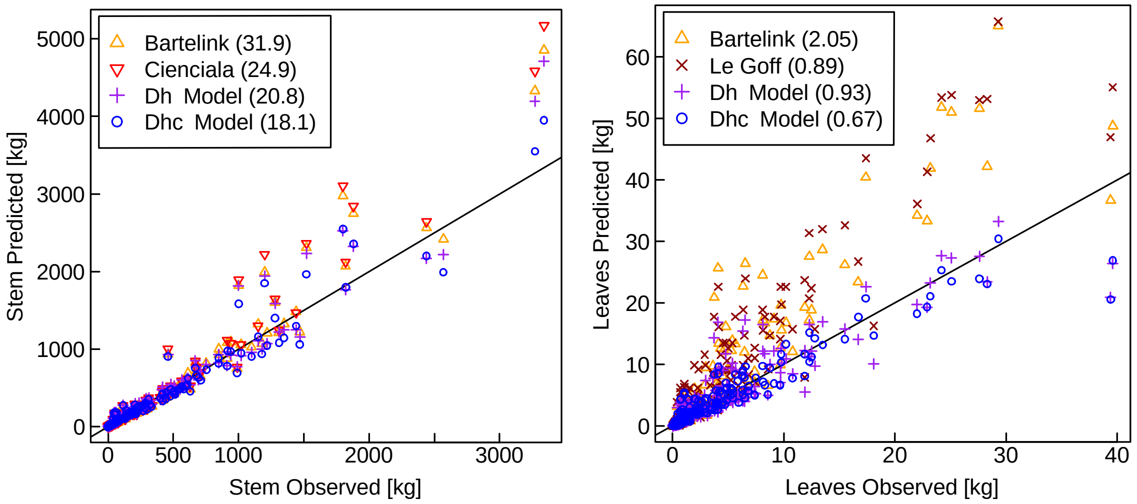

Figure 8 Predictions of the models fitted in the cross validation of a) stem and b) leaves biomass and comparison to previously published biomass functions. $m_{\text{stem}} = 0.0109 \cdot d^{1.951} \cdot h^{1.262}$ (Bartelink 1997) $m_{stem} = 0.014 \cdot d^{2.053} \cdot h^{1.084}$ (Cienciala et al. 2006). $m_{leaves} = 0.0167 \cdot d^{2.951} \cdot h^{-1.101}$ (Bartelink 1997) $m_{leaves} = \exp(-4.8599 + 2.1935 \cdot \ln(d))$ (Le Goff and Ottorini 2001). Values in brackets indicate the variance weighted RMSE.

and Clutter 2004), and biomass (Wirth et al. 2004b). Using non-linear mixed models allowed us to propagate different sources of variance and to analyse the structure of variance when scaling up from tree-level to aggregated level.

Our study illustrates the continuum between **fixed and random effects models.** When we compare models with and without additional covariates (dh and dhc-models), the contribution of the random effects to the total variance was much smaller in the dhc-models than in the dh-models (Figures 4 and 5). The effects of the covariates were formerly accounted for in part by the random effects in the dh-models. This finding corroborates the finding of Fang et al. (2001), where the inclusion of the predictor dominant height accounted for the differences between stands, that were formerly accounted for by random effects. The effect of covariates was less pronounced for the biomass compartments branch, brushwood, and stem biomass (Fig. 4). We hypothesize, that this is in part caused by the subjectivity involved in the separation of the stem and branch compartment and that thus there are inherently large differences between studies that are not due to environmental conditions but unknown differences in sampling protocols of different teams. This is confirmed by the fact that the random effects almost disappear for the sum of the two compartments (above ground woody biomass). In this context it is important to realize that the inclusion of covariates is only possible if – as in our case – data from many stands covering a range of ages and site conditions are pooled.

We generally observed that the random **effect of the variable 'study'** was small for biomass of stem, timber and above ground wood (Tables 4 and 5). This indicates that study-specific effects are relatively small compared to the dominating effect of the predictors diameter and height. Hence, the predictions of stem biomass did not vary much when we compared equations from different studies (Fig. 8a). However, we observed that models accounting for grouping effects in the residual variance performed better (eq. 7, Table 3). This implies that although the mean prediction was similar, the estimated variance of the biomass did vary between studies. The data, which were used in our study, do not allow us to distinguish whether this was an effect of differences in the sampling scheme between the studies, or a real effect of differences in growth variability between the studies. For other tree compartments, the random effects associated with the study were larger. Hence, for a specific new inventory, the biomass predictions will be more strongly biased towards the mean across studies. If a few additional biomass measurements for the new inventory are available it is possible to estimate the specific values of the random effects (e.g. Nothdurft et al. 2006). However, in most applications additional measurements of tree biomass compartments are too expensive. Lappi (1991) provides methods to estimate the values of the random effects of linear mixed-effects models for volume equations by related equations that require only diameter and height measurements. To develop similar related equations for the non-linear tree biomass equations presented here is beyond the scope of this paper and warrants further study.

Applying biomass functions from a single study outside the reference area will inevitable ignore the site influence on biomass allocation patterns (see discussion below) and will also underestimate variance (Fig. 6). This is, because the biomass function does not account for the differences between the studies, neither implicitly by random effects nor explicitly by covariates.

In the statistical analysis we assumed that the **measurement error** of the predictors does not have a profound effect on the estimation of the model coefficients (Table 5). Diameter, height, stand age, and altitude have been measured with high precision at the considered studies. For the covariate site index, which was in some cases estimated by age and height, we performed a Monte Carlo study for the above ground biomass where we varied the site index randomly with a standard deviation of ±1m and re-fitted the best dhc-model. The additional uncertainty introduced in the estimates of the model coefficients ranged only from 3% to 24% of the standard errors in Table 5 for the for coefficients β_1 and $\beta_{0.si}$ respectively. Hence, we conclude that the uncertainty in predictor site index has a sufficiently small effect on the results and does not change our interpretations.

Although certainly not all features of the models can be readily interpreted, some obvious **biologically plausible** patterns emerged that can be related to well-known allocation patterns thus increasing our confidence in the model predictions.

The three parameter model fitted the data of most biomass compartments best (Table 3). The better performance of the dh-models showed that the parameter tree height is an important additional predictor of biomass as observed in other studies for beech (Cienciala et al. 2006, Joosten et al. 2004, Zianis and Mencuccini 2003) as well as in studies of other species (Cienciala et al. 2006, Montagu et al. 2005). However, tree height did not significantly influence root biomass, as indicated by the best performance of the d2 model form (eq. 1). This corresponds to findings for Norway Spruce (Wirth et al. 2004b).

The parameter β_2 associated with the predictor tree height was negative for all crown compartments. This means, that (at a given diameter) higher trees tended to have a lower biomass of crown compartments. We think that this is most likely due to the fact that individuals with a high *h*/*d*-ratio tend to be suppressed trees with an elevated allocation to stem growth at the expense of allocation to crown biomass (Nilsson and Albrektson 1993, Vanninen et al. 1996, Wirth et al. 2004b). Negative values of β_2 have also been observed in a similar study on Norway spruce (Wirth et al. 2004b)

At a given diameter and height stem biomass increased with stand age in the best dhc-model. This may be related to a negative correlation between wood density and ring width (Bouriaud et al. 2004). At a given diameter and height older trees have more and thus smaller tree rings. This implies a higher wood density and hence higher biomass. The fact that the best model included also the site index and altitude as covariates with positive coefficients suggests additional environmental modulation of wood density that warrants further investigation.

Biomass equations are usually applied to make inferences at the **aggregated level**. For up-scaling, the sum of the biomass predictions of many single trees, e.g. within one stand, is calculated. When calculating the variance of the sum, prediction errors of the single trees are usually regarded as independent of each other for simplicity sake. Instead, our statistical approach accounts for covariances between prediction errors for several trees. The residuals of different trees are still considered independent. However, biomass predictions based on uncertain model coefficients deviate from the prediction that would result if the true (but unkown) model coefficients were used. The deviations of the predictions have the same direction for similar predictor values and therefore have a positive covariance (for a more formal description see Appendix A2). This issue is independent of using fixed-effects models, single-level random-effects models or multi-level mixed effects models. We showed how much the variance of biomass predictions at the aggregated level is underestimated when covariances between single tree-prediction errors are neglected (Fig. 7). This was already shown by exploring different assumptions about the covariances (Lehtonen et al. 2007, Lehtonen et al. 2004), however we provide the approach to actually quantify the covariances.

Further, we demonstrated that the reduction of variance upon scaling from tree level to aggregated level depends on the **partitioning of variance**. When differences between studies were represented explicitly by additional covariates instead of random effects, the relative contribution of fixed and random effects to total variance on tree level decreased (Fig. 4 background bars). Because of the linear scaling of the residual variance with the number of trees, the coefficient of variation (cv) of the predicted biomass at the stand level decreases with the square root of the number of trees if trees are regarded independent.

However, variance attributed to the uncertainty of fixed and random effects scale in a quadratic manner with the number of trees (Appendix A2), these partitions of variance became much more important at aggregated level. Hence, the decreased contribution of fixed and random variance at tree level with the inclusion of additional covariates led to a large decrease of total variance at aggregated level (Fig. 5 background bars). This finding highlights the importance to factor out variance components at the original, i.e. not log-transformed, scale.

Conclusions

This study presents generic biomass equations of seven biomass compartments for beech trees in Central Europe. A meta-analysis of biomass measurements of 443 trees of 76 sites from 13 studies across Central Europe enabled the assessment of the effect of the covariates age, site index, and altitude on tree biomass. Further, our study illustrates for the first time the importance of separating variance components (residual, fixed, random) in the context of scaling up uncertainties from tree to the aggregated level.

- Leaves and branch biomass prediction varied considerably across Central European studies. Using our large dataset for calibration improved model performance most for these compartments in comparison to previously published functions. Stem and above ground biomass did not vary this much, but still model performance slightly improved.
- In addition to mean predictions, also the variability of tree biomass differed between studies in Central Europe. Biomass functions based on a data set of a single study, did not account for the implicit differences between studies. Hence, using these functions outside the calibration area underestimates the variance of the prediction error for new biomass predictions.
- The covariates age, site index, and altitude modulated the effect of diameter and height. These additional variables accounted for a large part of the differences in biomass predictions between studies, which were otherwise accounted for by the random effects. Hence, the inclusion of these covariates increased model performance for several biomass compartments and reduced prediction variance.
- The predictions errors of trees are correlated, because of uncertain model coefficients. Neglecting these correlations when scaling up biomass to aggregated level underestimates prediction variance significantly. We developed equations and tools to quantify the covariances between single tree prediction errors as well as for up-scaling.

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Appendix A1: Variance of single predictions

The prediction $\hat{y}_{new}$ for a predictor vector x_{new}, covariates ν_{new} and an unknown group was done by applying the model formula to the vector of new predictors assuming zero random effects (expected value) and zero residual term.

In order to estimate the variance of the error of the non-linear prediction, we approximated the non-linear function f in equation 1 by its first order Taylor expansion in the parameter space around the estimated parameters $\hat{\beta}$ and $b = 0$ (eq. A1.1) (Gregoire and Schabenberger 1996).

[A1.1] $$f\left(x_{new}, \nu_{new}; \beta, b_{new}\right) \approx f\left(x_{new}, \nu_{new}; \hat{\beta}, 0\right) + u_{new}^{T}\left(\beta - \hat{\beta}\right) + w_{new}^{T}\left(b_{new} - 0\right)$$

where $u_{new} = \left.\frac{\partial f\left(x, \nu; \beta, b\right)}{\partial \beta}\right|_{x_{new}, \nu_{new}, \hat{\beta}, 0}$, and $w_{new} = \left.\frac{\partial f\left(x, \nu; \beta, b\right)}{\partial b}\right|_{x_{new}, \nu_{new}, \hat{\beta}, 0}$ are vectors of partial derivates evaluated at the estimated parameters $\hat{\beta}$, $b = 0$, and the values of predictors and covariate for the new observation.

Equation A1.1 describes the prediction that uses the true parameters β, and b_{new} by a prediction that uses the modified parameters $\hat{\beta}$ and $b = 0$ plus some deviation depending on the model parameters and the predictors. With this approximation the variance of the error of a non-linear prediction evaluates to eq. A1.2.

[A1.2] $$\begin{aligned} & Var\left(y_{new} - \hat{y}_{new}\right) \\ &= Var\left(f\left(x_{new}, \nu_{new}; \beta, b_{new}\right) + \varepsilon_{new} - f\left(x_{new}, \nu_{new}; \hat{\beta}, 0\right)\right) \\ &= Var\left(u_{new}^{T}\left(\beta - \hat{\beta}\right) + w_{new}^{T} b_{new} + \varepsilon_{new}\right) \\ &= u_{new}^{T} Var\left(\hat{\beta}\right) u_{new} + w_{new}^{T} Var\left(b_{new}\right) w_{new} + Var\left(\varepsilon_{new}\right) \\ &= u_{new}^{T} Var\left(\hat{\beta}\right) u_{new} + w_{new}^{T} \Psi w_{new} + \sigma^{2} \end{aligned}$$

Estimates for the unknown true covariance matrices $Var\left(\hat{\beta}\right)$ and Ψ as well for the residual variance σ^2 are obtained as a by-product of the numerical optimization algorithm used for REML estimation of the unknown parameters. The three terms of eq. A1.2 correspond to three components of variance, first the fixed effects, second the random effects, and third the residual variance.

To account for variance heterogeneity within groups, we modeled the residual variance as a power function of the predicted values (eq. A1.3).

[A1.3] $$Var\left(\varepsilon_{ij}\right) = \sigma^{2} \cdot \left|y_{ij}\right|^{2\delta}$$

If the coefficient δ of the power variance model additionally depended on the particular group ($\delta \rightarrow \delta_i$), the parameter δ_i for a new prediction was unknown because the group of the new prediction was unknown. The best estimate for the new prediction is the mean $\bar{\hat{\delta}}_i$ of the estimate for parameters δ_i. However, the mean-function appears in a non-linear term and a correction factor has to be applied. The general form of the expected value of a non-linear eq. $y = f(x)$ obtained by the delta-method is eq. A1.4 (Hilborn and Mangel 1997 p.58).

[A1.4] $$E(y) = f(E(x)) + \frac{1}{2} f''(E(x)) \cdot Var(x)$$

This leads in the case of eq. A1.3 ($f(\delta) = \sigma^{2} \cdot |y|^{2\delta}$) to eq. A1.5.

[A1.5] $$\begin{aligned} \hat{Var}\left(\varepsilon_{new}\right) &= \sigma^{2} \cdot \left|y_{new}\right|^{2\bar{\hat{\delta}}_i} + 2\sigma^{2}\left(\ln\left|y_{new}\right|\right)^{2}\left|y_{new}\right|^{2\bar{\hat{\delta}}_i} \cdot Var(\hat{\delta}_i) \\ &= \sigma^{2} \cdot \left|y_{new}\right|^{2\bar{\hat{\delta}}_i}\left(1 + 2\left(\ln\left|y_{new}\right|\right)^{2} \cdot Var(\hat{\delta}_i)\right) \end{aligned}$$

Appendix A2: Variance of the sum of predictions

Many applications of statistical models calculate the sum of several individual predictions that originate from the same group (e.g. sum of biomass of individual trees measured by the same team with the same measurement procedure). The expected value of the sum of *n* predictions is simply the sum of the single expected values, i.e. model predictions. However, the variance of the sum of prediction errors has to account for covariances between the individuals. The variance of the sum of prediction errors is given by eq. A2.1

$$\begin{aligned}
&Var\left(\sum_{j}^{n}\left(y_j-\hat{y}_j\right)\right)\\
\text{[A2.1]}\qquad &=\sum_{j}^{n}Var\left(y_j-\hat{y}_j\right)+2\sum_{j}^{n}\sum_{k=j+1}^{n}Cov\left(y_j-\hat{y}_j,y_k-\hat{y}_k\right)\\
&=\sum_{j=1}^{n}\sum_{k=1}^{n}Cov\left(y_j-\hat{y}_j,y_k-\hat{y}_k\right)
\end{aligned}$$

where $Cov\left(y_j-\hat{y}_j,y_k-\hat{y}_k\right)$ denotes the covariance between the errors of the individual prediction for the new observations *j* and *k*.

In the following we derive the covariance between two prediction errors for predictions based on model of eq. 5 within the same group *i*. With approximating model eq. 5 by its first order Taylor expansion (eq. A1.1) around $\hat{\beta}$ and $b\ \ = 0$ we derive eq. A2.2.

$$\begin{aligned}
&Cov\left(y_{new,1}-\hat{y}_{new,1},y_{new,2}-\hat{y}_{new,2}\right)\\
&\approx Cov\begin{pmatrix} f\left(x_{new,1},v_{new,1},\hat{\beta},0\right)+u_{new,1}^{T}\left(\beta-\hat{\beta}\right)+w_{new,1}^{T}b_{new}+\varepsilon_{new,1}-f\left(x_{new,1},v_{new,1},\hat{\beta},0\right)\\ ,f\left(x_{new,2},v_{new,2},\hat{\beta},0\right)+u_{new,2}^{T}\left(\beta-\hat{\beta}\right)+w_{new,2}^{T}b_{new}+\varepsilon_{new,2}-f\left(x_{new,2},v_{new,2},\hat{\beta},0\right)\end{pmatrix}\\
\text{[A2.2]}\quad &=Cov\left(u_{new,1}^{T}\left(\beta-\hat{\beta}\right)+w_{new,1}^{T}b_{new}+\varepsilon_{new,1},u_{new,2}^{T}\left(\beta-\hat{\beta}\right)+w_{new,2}^{T}b_{new}+\varepsilon_{new,2}\right)\\
&=Cov\left(u_{new,1}^{T}\left(\beta-\hat{\beta}\right),u_{new,2}^{T}\left(\beta-\hat{\beta}\right)\right)+Cov\left(w_{new,1}^{T}b_{new},w_{new,2}^{T}b_{new}\right)+Cov\left(\varepsilon_{new,1},\varepsilon_{new,2}\right)\\
&=u_{new,1}^{T}Var\left(\hat{\beta}\right)u_{new,2}+w_{new,1}^{T}Var\left(b_{new}\right)w_{new,2}+0\\
&=u_{new,1}^{T}Var\left(\hat{\beta}\right)u_{new,2}+w_{new,1}^{T}\Psi w_{new,2}
\end{aligned}$$

where $u_{new,1},u_{new,2},w_{new,1}$, and $w_{new,2}$ are vectors of partial derivates as explained with eq. A1.1. Estimates for the unknown true covariance matrices $Var\left(\hat{\beta}\right)$ and Ψ are obtained as a by-product of the numerical optimization algorithm.

If the two observations were of different groups, i.e. trees of different regions and measured by different teams, the covariance in prediction errors due to random effect would be zero, i.e. $Cov\left(w_{new,2}^{T}b_{new,1},w_{new,2}^{T}b_{new,2}\right)=0$.

Now we are ready to calculate and interpret the variance of a sum of prediction errors of model eq. 5. Inserting eq. A2.2 into eq. A2.1 leads to eq. A2.3.

$$\text{[A2.3]}\qquad Var\left(\sum_{j}^{n}\left(y_j-\hat{y}_j\right)\right)=\sum_{j}^{n}\sum_{k}^{n}\left(u_j^{T}Var\left(\hat{\beta}\right)u_k+w_j^{T}\Psi w_k\right)+\sum_{j}^{n}Var\left(\varepsilon_j\right)$$

Similar to the variance of single predictions (eq. A1.2), eq. A2.3 is composed of the three terms of the components of variance (fixed, random, and residuals). However, the residual variance occurs in a simple sum over all individuals, whereas the fixed and random terms occur within a sum of sums. Hence the residual variance increases linearly with the number of individuals, whereas the random and fixed components of variance increase quadratically with the number of individuals.

The covariance terms in eq. A2.3 can be negative. Hence, they potentially cancel out each other. However, individuals of the same group often have similar predictor values and have positive covariances.

Appendix A3: Application example

In the following example, we demonstrate how to use the presented models and equations to calculate a new prediction for stem biomass and its confidence interval for a single tree with diameter (*d* = 18.8 cm), height (*h* =16.9 m) age (*age* = 40 years), site index (*si* = 30 m), and altitude (*alt* = 470 m). Consequently, we choose the dhc-model, because all the additional covariates are known. The label dh3 in table 5 indicates that the basic model form is $m_{new} = c_0 d^{c_1} h^{c_2}$ (eq. 3). Site index, age, and altitude affect the coefficient c_0, and table 6 indicates that the model includes also random effect in c_0: $c_0 = \beta_0 + b_{0,i} + \beta_{0,age} \cdot age + \beta_{0,si} \cdot si + \beta_{0,alt} \cdot alt$ (eq. 4c). The other coefficients do neither include covariates nor a random effect. Hence the full equation of above ground biomass for tree *j* is given by eq. A3.1.

$$[\text{A3.1}] \quad m_{New} = f(d,h,age,si,alt;b) = \left(\beta_0 + b_{0,i} + \beta_{0,age} \cdot age + \beta_{0,si} \cdot si + \beta_{0,alt} \cdot alt\right) d^{(\beta_1)} h^{(\beta_2)}$$

Hence, with setting the random effect $b_{0,i}$ to its expected value 0 for a general prediction, the stem biomass computes to (0.00351 +0 +3.47E-05*40+6.72E-04*30 +8.11E-06*470) *18.8^1.84 *16.9^1.04 = 121 kg. The variance of the prediction error is estimated according to eq. A1.2 and A1.5 as

$$Var(\hat{m}_{new} - m_{new}) =$$

$$\begin{bmatrix} \underbrace{4250.244}_{\frac{\partial f(d,h,age,si,alt;b)}{\partial \beta_0}} & \underbrace{127507.3}_{\frac{\partial f}{\partial b_{0,si}}} & \underbrace{170009.8}_{\frac{\partial f}{\partial \beta_{0,age}}} & \underbrace{1997615}_{\frac{\partial f}{\partial \beta_{0,alt}}} & \underbrace{360.0897}_{\frac{\partial f}{\partial \beta_1}} & \underbrace{347.013}_{\frac{\partial f}{\partial \beta_2}} \end{bmatrix} Var\left(\hat{\beta}\right) \begin{bmatrix} 4250.244 \\ 127507.3 \\ 170009.8 \\ 1997615 \\ 360.0897 \\ 347.013 \end{bmatrix}$$

$$+ \begin{bmatrix} \underbrace{4250.244}_{\frac{\partial f(d,h,age,si,alt;b)}{\partial b_{0,i}}} \end{bmatrix} \Psi [4250.244]$$

$$\underbrace{+ \overbrace{0.0903}^{\sigma^2} \cdot \left| \overbrace{122.7360}^{\hat{m}_{new}} \right|^{2 \cdot \overbrace{0.842}^{Mean(\delta)}} \left(1 + 2 \ln^2 \left(\overbrace{122.7360}^{\hat{m}_{new}} \right) \cdot \overbrace{0.0196}^{Var(\delta)} \right)}_{Var(\varepsilon_{new})}$$

$$= 30.3 + 179.9 + 568.6 = 778.9$$

Where *f* is given by eq. A3.1, $Var\left(\hat{\beta}\right)$ is the estimated 6x6 covariance matrix the estimated fixed effects, Ψ is the 1x1 random effects covariance matrix[6]. The values of the coefficients of the third term are given in Table 6. A symmetric 95% confidence interval around the prediction is calculated using the quantile of the standard normal distribution as $\pm 1.96 \cdot \sqrt{Var(\hat{m}_{new})}$. This becomes 54.7 kg and the 95% confidence interval ranges from 68 kg to 177 kg.

We provided R-objects[7] of all the best models together with coefficients, gradient functions, the fixed and random effects covariance matrices and functions to calculate the variance of single tree biomass predictions (nlVar). The results of this example are simply obtained with the R-Command: "`nlVar(dhcme.beech$stem, data.frame(dbh=18.8, height=16.9, age=40, si=30, alt=470), pred=TRUE)`".

Similarly, for a group of trees the predicted biomass and the variance of the prediction error are simply obtained with the provided R-function nlCovar[8].

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[6] Both matrices are made available with electronic supplementary material S4

[7] Electronic supplementary material S5

[8] An example of calculating biomass and prediction variance at stand level is in electronic suppl. material S6

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Modelling Mean Above and Below Ground Litter Production Based on Yield Tables

Abstract Estimates of litter production are a prerequisite for modeling soil carbon stocks and its changes at regional to national scale. However, the required data on biomass removal is often available only for the recent past. In this study we used yield tables as a source of probable past forest management to drive a single tree based stand growth model. Next, simulated growth and timber volume was converted to tree compartment carbon stocks and biomass turnover. The study explicitly accounted for differences in site quality between stands. In addition we performed a Monte-Carlo uncertainty and sensitivity analysis. We exemplify the approach by calculating long-term means of past litter production for 10 species by using yield tables that have been applied in Central Germany during the last century. We found that litter production resulting from harvest residues was almost as large as the one from biomass turnover. Differences in site quality caused large differences in litter production. At a given site quality, the uncertainty in soil carbon inputs were 14%, 17%, and 25% for Beech, Spruce, and Pine stands, respectively. The sensitivity analysis showed that the most influential parameters were associated with foliage biomass and turnover. We conclude that rates of mean past litter production and their uncertainties can reliably be modeled on the basis of yield tables if the model accounts for (1) full rotation length including thinning and final harvest, (2) differences in site quality, and (3) environmental dependency of foliage biomass and foliage turnover.

Keywords soil carbon, yield table, litter production, biomass turnover, harvest residues, thinning, Spruce, Beech, Pine, uncertainty, sensitivity analysis, forest management

Introduction

Estimates of litter production are a prerequisite modeling forest soil carbon stocks and its changes. Most dynamic soil carbon models of mineral forest soils are driven by carbon inputs from plant litter production, which is usually estimated by forest inventories (de Wit et al. 2006, Liski et al. 2006, Ågren et al. 2007). The combination of forest inventories and modeling is a viable option to compile soil carbon stock changes from regional to national and global scales (Peltoniemi et al. 2007). Models, which allow for reliable estimates of changes in soil carbon stocks at different spatial scales, are of particular interest, because they could be used for national annual greenhouse gas reports according to the UN Framework Convention on Climate Change and the Kyoto Protocol (UNFCCC 1997). An additional important use case of estimates of litter production baselines is to infer the sustainability of intensively managed energy plantations with respect soil carbon protection (Reijnders 2006). The derivation of long-term mean litter input rates requires data on forest biomass and on past forest thinning operations and harvest. For many regions, these data are available for the recent past only. A model for forest timber volume, yield and growth under defined site conditions and a defined management

List of Symbols

dbh	diameter at breast height (1.3m)
h	tree height (m)
si	site index (m)
ς	stem wood density (t/m³)
l_P	litter production for litter compartment p (tC/ha/yr)
p	litter compartment (fine root, foliage, etc.)
i	index of ration periods
t_i	length of simulation period i (yr)
ce	carbon per timber volume (tC/m³ dry wood)
b_j	regression coefficients

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regime is recorded in yield tables, which are used in this study as an approximation tool of former forest management.

Yield tables were developed for many species, many site classes, and many regions (e.g. Tjurin and Naumenko 1956, e.g. McArdle 1961, Nishizono et al. 2005). They list expected stand characteristics such as tree height, basal area, and standing timber volume, as well as proposed timber volume of thinning and harvesting for several stand age classes and tree species. Because of environmental changes over the last 50 to 60 years some older yield tables do not reflect current tree growth (Mund et al. 2002, Jandl et al. 2007). However, their common use in forestry practice and for forest planning indicate their usefulness at least in the past.

The objective of this study is to demonstrate how yield tables can be used to estimate long-term means of past litter production. This proposed methodology is significant for all studies on soil carbon balance where no better data on former forest management or biomass is available. The intended spatial scale is the regional level with calculations based on single stands or single strata of the forested area. We investigate the following questions: (1) How relevant is litter production resulting from self-thinning, precommercial thinning, commercial thinning, and final harvest compared to litter production resulting from foliage, fine roots, and branches turnover? (2) How large is the influence of different tree species and of different site qualities on the estimates of litter production? And (3) how large are the uncertainties of the estimates and which factors contribute most to them?

We exemplify the approach using yield tables that have been applied to forests in Eastern Germany (Nicke 1997) to drive a forest growth model and convert simulated timber volume and harvest to rates of litter production. Further we study the uncertainty of the results and the sensitivities to parameters and assumptions.

Methods

An overview of the general approach of this study is given in Fig. 1. The details are explained in the following sections.

Yield tables and study area

We used yield tables as a source of data on probable past forest management. In general, yield tables describe the ''regular growth'' of forest stands for: (1) distinct tree species; (2) under constant environmental conditions; (3) according to a defined management regime. In a first step, we compiled a relational database of yield tables, which provides amongst others the following attributes.

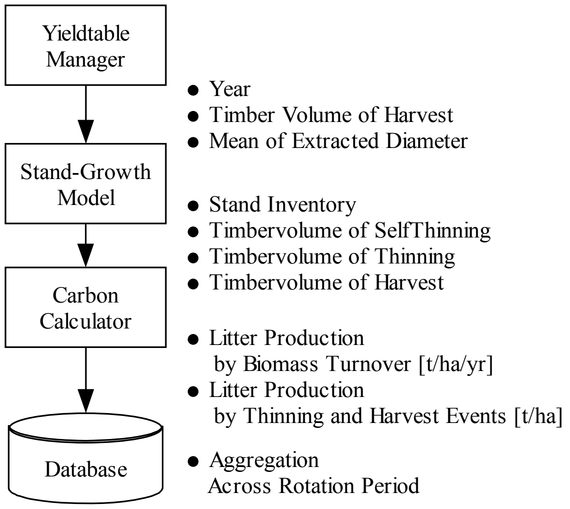


Figure 1: Overview of modeling mean litter production by yield tables. Information on forestry management, as represented by yield tables, and was used to drive a stand growth model. The model outputs were used to calculate litter production by biomass turnover and management operations during stand growth. Finally, the outputs were aggregated across one rotation period.

- meta information: region, where the data that was used to construct the table data was collected, genus and species, and citation
- absolute site index: the expected height of trees (m) at stand age 100 years (Kramer and Akça 1995)
- stand attributes: stand age (yr), dominant height (m), basal area (m^2), tree number per hectare (1/ha), and timber volume (m^3/ha), quadratic mean of tree diameters at breast height (dbh) (cm), and stand height (m)

The database currently contains 228 yield tables out of 49 yield table collections. Each yield table collection contains several tables corresponding to different site qualities. Site quality is expressed by the site index as defined above. In this study we used yield tables that have been applied in the past in Eastern Germany (Table 1). Hence, the study area of the application example is defined by the set of stands, where these yield tables have guided the management, which comprises most of the forest area of Eastern Germany. The approach of inferring biomass removal by yield tables can be extended to other regions in a straightforward way, by using the yield tables that have been applied in the corresponding region.

Table 1: Yield tables that have been used in this study to simulate standard rotation and litter inputs. Several site indices were used. Additionally the table lists the prescribed rotation length and the stand age from which commercial thinning with biomass removal was applied. a) taken from (Nicke 1997). b) % of rotation period

Tree group	Yield (mostly grey literature)	Site Index [m]	Length of Rotation Period [yr]	Begin of Biomass removal^b
Spruce	Wenk et al. (1985) (a)	36/30/24	120/120/130	40
Beech	Dittmar et al. (1986) (a)	36/30/24	160/160/160	40
Pine	Lembcke et al. (1976) (a)	32/26/20	130/130/140	40
Oak	Ertelt (1962) (a)	23.4/20/15.7	200/200/160	30
Larch	Schober R (1987) (a)	34/29.5/25	140/140/140	40
Douglas fir	Bergel (1985) (a)	43.8/38.7/34.1	100/100/100	40
Linden/Maple	Böckmann (1990)	33.5/29.2/23.1	90/120/120	60
Birch	Tjurin and Naumenko (1956) (a)	31.8/25.1/17.1	100/100/90	40
Ash	Wimmenauer (1919) in (Erteld 1962) (a)	29.9 / 24.8	120/120	40
Poplar	Knapp (1973) in (Autorenkollektiv 1982) (a)	37/30.5/24.1	50/50/50	70

Stand development simulations

Stand development was simulated with the TreeGrOSS model (Nagel 1999, Nagel 2003). The empirical stand growth model simulates diameter and height development of single trees and explicitly takes account for competition. By these simulated competition indices also self-thinning is simulated.

The stand was initialized according to the first age that was recorded in the yield table and had a tree diameter (dbh) ≥ 7cm. We implemented thinning and harvesting operations according to the yield tables in the following way. We simulated tree growth with environmental conditions of the former century, which well matched the growth recorded in the yield tables. Tree growth was simulated in periods of at most 5 years. Shorter periods occurred when the time to the next date that was recorded in the corresponding yield table was less than 5 years. We simulated tree dimensions before the growing season. In each of these simulation cycles, first growth was projected, next self-thinning during this period was calculated, and finally thinning was applied. Basal area of thinned trees was derived by comparing the yield table target basal area with the simulated basal area. Type of thinning (from above/below/neutral) was determined by comparing diameter from yield table with the simulated diameter. We assumed a clearcut of the stand at the last age that was listed in the corresponding yield table. In addition we specified the stand age until precommercial thinning has been applied by a fraction of the rotation period (Table 1). At precommercial thinning all biomass is left in the forest, at commercial thinning a defined fraction of branches and stem is removed from the forest.

Calculation of litter production by tree biomass turnover

Yield tables and the stand growth model provided data on timber volume. Our focus, however, was on litter production, which originated from biomass turnover of all tree compartments. Hence, the timber volume was converted to dry timber biomass by species specific basic wood densities. Next, biomass of different tree compartments were estimated by multiplying timber biomass by site and age specific conversion factors. For spruce we used the functions developed for Central Europe (Wirth and Schumacher 2002, Wirth et al. 2004) and for pine the functions developed for Finish forests (Lehtonen et al. 2004a). For beech, only conversion factors for whole tree carbon stock were available. Hence, we re-examined the dataset of Wirth et al. (2004) to derive expansion factors for other tree compartments as well (Table 2). The factors depend on species, stand age, and site quality. Finally, biomass stocks were converted to carbon stocks by species specific carbon concentrations. Biomass of other tree species was calculated using conversion factors of either spruce, pine, or beech, but using species specific dry wood densities and carbon contents. Basic wood densities and carbon contents were taken from Weiss et al. (2000).

The above ground litter production was derived by multiplying branch and foliage biomass by a mean turnover time (Table 3). We did not calculate the turnover of stem and coarse root because this was accounted for by self-thinning, thinning and harvest. The production of below ground litter was derived by multiplying the above ground litter production by a species specific factor (Table 3). For Pine and Spruce forests we adapted the factor 1.5 from Ågren et al. (2007). We did not find a similar study for beech. However, in a first approximation we assumed that the soil carbon inputs by litter production are balanced by outputs by soil respiration, i.e. the storage is very small compared to the input/output fluxes. Bowden et al. (1993) found that 37% of the annual soil respiration of a North American broadleaved forest can be attributed to above ground litter and 30% to belowground litter. A more recent study confirms this ratio of about 0.8 of below ground to above ground litter production but indirectly infers an additional carbon flow from roots to rhizosphere (Fahey et al. 2005). Because our focus is on soil carbon inputs by litter production, we included this flux in the below ground litter production and used a ratio of 1.0 for beech.

Our aim was to come up with a mean of litter production across the entire rotation cycle. Hence, we aggregated the litter input rates of all the simulation periods by Eq. 1.

$$\bar{l}_p = \frac{\sum_i \frac{1}{2}\left(l_{p,i-1} + l_{p,i}\right) \cdot t_i}{\sum_i t_i} \qquad (1)$$

In Eq. 1 the absolute amount of litter production for each simulated period *i*, was calculated by multiplying the mean rate of litter production of this period $\frac{1}{2}\left(l_{p,i-1} + l_{p,i}\right)$ by the length of the period t_i. Finally the sum of the litter across all simulation periods was divided by sum of the length of all simulation periods, i.e. the rotation length.

Table 2: Coefficients and standard errors of the conversion-expansion factor function $ce_{Beech} = b_0 + b_1 e^{-b_2 \cdot Age}$ (t C/m³ dry wood), stratified by tree compartment and site index. si: Site indices 0: across all, 1 good (>=28m), 2 average (20..28m), 3 low (<20m); rmse: root mean square error of the residuals; cv: rmse / mean(ce_{Beech})

p	si	b0	b1	b2	rmse	cv
total	0	0.741	0.636	0.018	0.113	12.7%
	1	0.735	1.320	0.020	0.152	14.6%
	2	0.760	0.649	0.022	0.079	9.2%
	3	0.827	0.922	0.067	0.065	7.2%
stem	0	0.479	0.380	0.020	0.073	8.2%
	1	0.445	0.765	0.021	0.155	14.9%
	2	0.464	0.289	0.014	0.052	6.0%
	3	0.530	0.496	0.050	0.042	4.7%
branches	0	0.137	0.235	0.037	0.044	5.0%
	1	0.164	0.361	0.027	0.054	5.2%
	2	0.142	1.341	0.091	0.029	3.4%
	3	0.107	0.274	0.054	0.026	2.9%
leaf	0	0.005	0.107	0.042	0.005	0.6%
	1	0.004	0.137	0.033	0.005	0.4%
	2	0.006	0.286	0.075	0.002	0.3%
	3	0.006	0.141	0.067	0.001	0.1%
root	0	0	0.185	0.002	0.292	32.7%
	1	0	0.258	0.004	0.189	18.1%
	2	0	0.199	0.003	0.281	32.6%
	3	0	0.118	-0.004	0.301	33.5%

Calculation of litter production by thinning and harvesting events

In addition to litter production by foliage, fineroot, and branch turnover, also self-thinning and residues after harvesting or thinning operations contribute to litter production and carbon inputs to the soil (Harmon et al. 1996,

Table 3: Coefficients for estimating biomass turnover. Numbers in brackets denote the standard deviation, used in the sensitivity analysis (a) (Muukkonen and Lehtonen 2004) with assuming standard deviation of 1/2 of the range to minimum; (b) (Ågren et al. 2007); (c) (Heinsdorf et al. 1993); (d) based on equation 4 from (Lehtonen et al. 2004b); mean across trees with dbh from 7 to 40 cm; (e) all leaves biomass is shed each year unless some carbon that is translocated before leaves senescence (f) based on data of (Mund 2004) (g) based on (Bowden et al. 1993) and (Fahey et al. 2005)

Species	Turnover [1/yr]		Bel.gr / Abv.gr. litter production
	Foliage	Branches	
Spruce	0.10 (0.015) (a)	0.0125 (0.008) (a)	1.5 (0.3) (b)
Pine	0.4 (0.1) (c)	0.015 (0.01) (d)	1.5 (0.3) (b)
Beech	0.9 (0.09) (e)	0.013 (0.01) (f)	1.0 (0.2) (g)

Nishizono et al. 2005). In each simulation period the stand growth model simulated the timber volume of a) trees that died by self-thinning, b) trees cut by precommercial thinnings, and c) trees extracted by commercial thinning and harvest. Carbon stocks of tree compartment of tree volumes a) and b) were calculated with previously presented conversion factors. We excluded foliage and fineroot carbon stocks from input to the soil to avoid double counting with turnover. This led to a small underestimation of litter input rates for coniferous trees.

During commercial thinning and harvest a part of the stem and branch biomass is removed and another part is left at the side as harvest residues. Information about the proportion of the removed wood is based on timber volume and does not distinguish between stem and branch. At coarse scale removal statistics can be used to obtain extracted timber volume (Dieter and Elsasser 2002). However, at stand scale, we used values of a guideline of the forest administration (Weber 2003) to interpolate proportion of the removed timber volume by species and stand age (Fig. 2).

The carbon in harvest residues was calculated in the following way. We multiplied the sum of stem and branch carbon by proportion of removed timber wood (Fig. 2). Next we partitioned the remaining carbon to fine woody litter and coarse woody litter with the proportions 40% and 60% respectively. We did not find suitable studies to back up this subjective partitioning. However, we will discuss with the sensitivity analysis that changes in this partitioning do not affect the resulting equilibrium soil carbon stocks very much. All the litter produced by thinning/harvesting events were summed over the rotation period and divided by the rotation length to obtain a mean annual rate of litter production.

Uncertainty analysis

Uncertainty of the calculated litter production was studied by the Monte Carlo method. This method investigates the distribution of a random variable by simulating random numbers (Gentle 1985). In our case the random variable, in which we are interested in, is the sum litter production over all litter compartments and the simulated random numbers represent the uncertain parameters that were used to calculate litter production. Monte Carlo simulation involves the generation of a large number of realizations of the parameters from their joint probability distribution. The distribution of the calculated results, i.e. rates of litter production, across all the realizations of parameters represents the result's empirical joint probability distribution. This empirical distribution can be used to describe the uncertainty of the result.

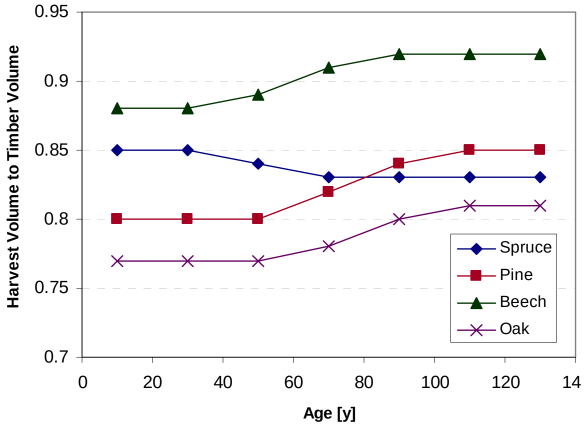


Figure 2: Regional estimates of extracted timber volume in relation to timber volume of trees that died during commercial thinning operation according to Weber (2003). Having regional species and age-specific estimates of this factor improves the estimate for the litter production resulting from harvest residues.

We studied the propagation of the uncertainty of converting timber volume to carbon stocks in stem, branch, foliage, and root by varying the product of expansion-factor, wood density, and carbon content. In the following we refer to this product by the term conversion-expansion factor (ce-factor) (Table 4). The precision of the ce-factor is dominated by the biomass expansion factor. The precision listed in Table 4 actually describes the uncertainty of predicting an intermediate expansion factor for a given combination of site factors such as stand age and site quality. We also included uncertainty of biomass turnover by varying the mean lifetime of foliage and branches and by varying the proportion of belowground litter input. In addition we included uncertainty of information on management to our analysis by varying the proportion of removed timber, the proportion of remaining coarse wood that is collected for firewood, and the proportion of fine wood in harvest residues. We prescribed a log-normal distribution for each parameter with a mean according to standard parameterization and a coefficient of uncertainty (*cv*) according to Table 4. The mean of simulated litter production varied less than 0.3% after 4000 runs. Hence we used 5000 runs for one Monte-Carlo simulation. In a first scenario we assumed all parameters to be independent. In a second scenario we introduced positive correlations between the ce-factors of stem, root, and foliage, and a negative correlation

Table 4: Coefficient of uncertainty (standard deviation divided by the mean) of the parameters used in the uncertainty analysis. ce: conversion-expansion factor: product of wood density, carbon content, and expansion-factor from timber mass to mass of tree compartment. (a) according to table 3 (b) G. Weber pers. communication, see also Fig 2 (c) unknown, reasonable number (d) unknown, conservative number (e) (Wirth et al. 2004) with regional density error and site specific factors (f) according to table 3 in (Lehtonen et al. 2004a) (g) medium site index of Table 2.

	Spruce	**Pine**	**Beech**
Biomass to Carbon Conversion			
ce of Stem	13.3% (e)	5.3% (f)	6.0% (g)
ce of Branch	13.3% (e)	9.7% (f)	3.4% (g)
ce of Foliage	13.3% (e)	25.9% (f)	0.3% (g)
ce of Root	13.3% (e)	11.3% (f)	33.0% (g)
Biomass Turnover			
lifetime of branches (a)	63.0%	67.0%	70.0%
lifetime of foliage (a)	15.0%	25.0%	10.0%
proportion of below ground to above gr. litter (a)	20.0%	20.0%	25.0%
Thinning and Harvest			
proportion of extracted timber on harvest (b)		5.0%	
proportion of collected remaining coarse wood (c)		25.0%	
proportion of fine wood in harvest residues (d)		30.0%	

between the ce-factors of stem and branches. The correlations at the scale of the normal distribution were 0.7 and -0.4 respectively. This reflected our experiences from examining uncertainty with constructing biomass functions for Common beech (Wutzler and Wirth 2007).

Sensitivity analysis

The data generated by the Monte Carlo simulation was also used to assess which parameters had the largest influence on the uncertainty of litter production. We assessed the importance of each parameter by calculating the rank-based correlation, called spearman's rho (Conover 1980), between each input parameter and the calculated litter production. The strength of this correlation reflects how strongly the parameter influences the uncertainty in the results (Vose 1996). In order to compare the correlations we normalized the squared correlation to 100%. We refer to this value as importance index.

In addition to the Monte Carlo study, we investigated how the uncertainty of stand growth affected the litter production. We represented the uncertainty of stand growth by varying the site index. The soil carbon inputs for the uncertain site index were linearly interpolated between the site indices, for which the soil carbon inputs have been calculated previously from yield tables.

Comparison with measured leaves litterfall

To validate our model results we compared the estimated litter production by leaves turnover with measured litter fall data of a case study on European beech forests (Fagus sylvatica L.) in Thuringia, Germany, under different silvicultural management (regular shelterwood system, selection system, unmanaged forest; Mund (2004). In that study annual litter fall of two years was measured by litter traps at four study sites each including 3 or 5 forest stands. The mass of leaf litterfall was converted to carbon by measured carbon contents. Growing conditions are described as optimal for beech forests and corresponding to site indices above 28m.

Results

The three major sources of litter production, which were investigated in this study, were continuous biomass turnover, self-thinning, and residues remaining after thinning operations and harvest. Simulated self-thinning differed between species. For Spruce and Beech stands, which were dominating at the study area, carbon inputs from self-thinning was negligible compared to harvest and thinning residues.

The comparison of litter production by species revealed large differences (Fig. 3). The comparison also confirmed that the sum of litter production resulting from thinning and harvest was smaller but of the same magnitude as the sum of litter production by turnover of foliage, fine root, and branches across the rotation period. In the comparison of litter production by different litter compartments, the largest contributions were found with fine root litter production, followed by foliage litter production (Fig. 4). Branch turnover contributed minor parts only.

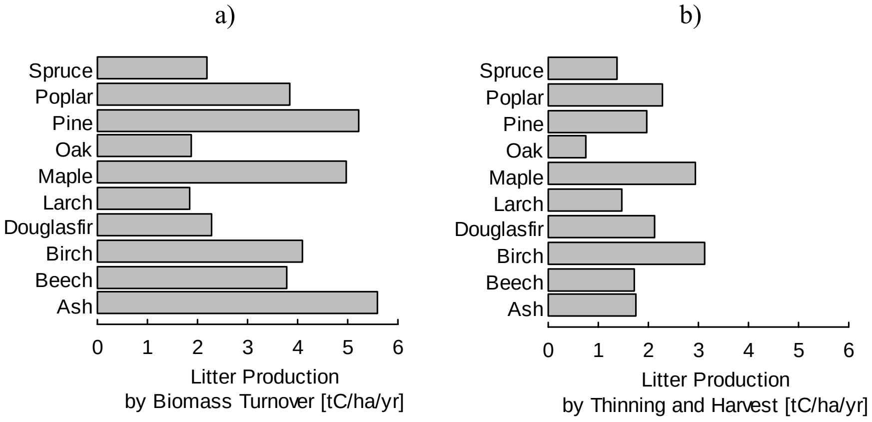


Figure 3: Comparison of litter production between different monospecific stands of medium site quality. Litter production by the biomass turnover (a) are of the same magnitude as litter production by thinning events (b) for all species. Differences between species are of the same magnitude as the litter production itself.

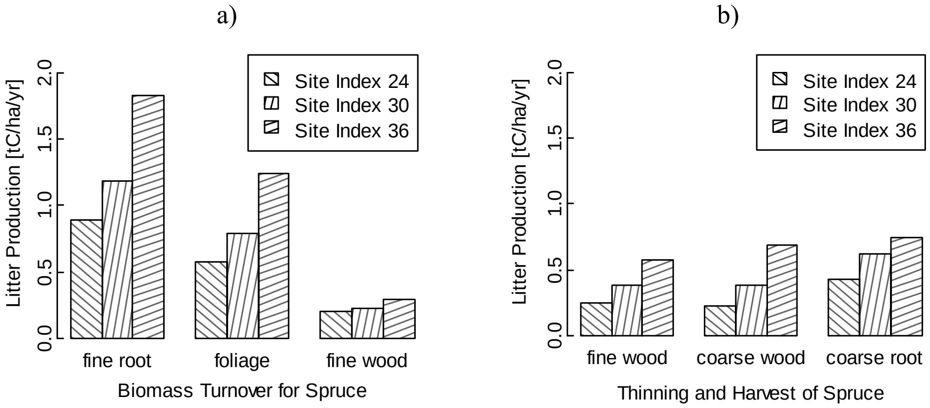


Figure 4: Comparison of litter production between different site qualities (site index) by litter compartments for spruce. The difference in litter production between site qualities is of the same magnitude as the litter production itself.

When comparing litter production by site quality, we found that differences were in the same magnitude as the mean for all compartments (Fig. 4). The calculated litter production for the three most important species for three different site qualities are listed in Table 5.

In the following presentation of the results of the Monte-Carlo uncertainty analysis, we concentrate on the sum of litter production across all litter compartments. Fig. 5 displays the resulting empirical distribution of two Monte-Carlo simulations for Spruce of site index 30m.

Table 5: Calculated litter production (tC/ha/yr).

		Turnover			**Thinning and Harvesting**		
Species	Site Index	Foliage	Fine Root	Branches	Fine Wood	Coarse Wood	Coarse Root
Spruce	24.0	0.57	0.89	0.20	0.25	0.22	0.43
	30.0	0.79	1.18	0.22	0.38	0.38	0.62
	36.0	1.25	1.83	0.30	0.57	0.69	0.74
Pine	20.0	1.46	1.96	0.13	0.24	0.74	0.53
	26.0	2.15	2.87	0.19	0.31	0.95	0.70
	32.0	2.88	3.83	0.25	0.40	1.22	0.90
Beech	24.0	0.77	0.89	0.24	0.23	0.24	0.52
	30.0	1.56	1.79	0.42	0.42	0.48	0.81
	36.0	2.15	2.45	0.55	0.65	0.81	1.15

The first simulation was performed with sampling from a parameter distribution that assumed independent parameters, the second one from a parameter distribution that included correlations between the parameters. From the first distribution, we calculated a mean litter production of 3.9 tC/ha/yr, a standard deviation of 0.65 tC/ha/yr, giving a coefficient of uncertainty (cv) of 17%. The variance of the second simulation did not differ from the first simulation within two significant digits. Similarly, we inferred a cv of 14% and 25% for Beech and Pine respectively from their empirical distributions. These uncertainties were in the same magnitude as the uncertainty of stand growth, as represented by a 5% increase of the site index.

The comparison of the importance index, a combined measure of parameter uncertainty and parameter sensitivity, provided a measure of the relative importance of the parameters for the uncertainty in the soil carbon inputs. Fig. 6 displays the importance index for all the parameters that were included in the sensitivity analysis. Uncertainty of foliage turnover (lifeTimeFoliage) was an important cause of the uncertainty in litter production for all species. Contrary, uncertainty in harvest information (harvest, pWoodPicke, fwlShare) was not important with all species. For Pine, the comparatively high uncertainties of both, expansion factor for foliage and mean lifetime of

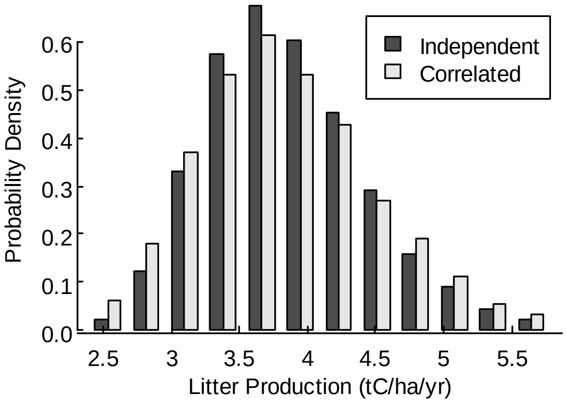


Figure 5. Histogram litter production for Spruce of site index 30m when accounting for uncertainty in model parameters. The distribution deviates slightly from normal by having a stronger positive tail. In the case where correlations between input parameters were accounted for, the distribution has slightly stronger tails.

foliage (Table 4) were important causes of the large uncertainties in the result and are dominating over all the other factors.

We further studied how the uncertainty of litter production would decrease if we were able to better constrain foliage biomass and turnover. We repeated the Monte-Carlo-Analysis with double precision of the ke-factor for foliage and double precision of the foliage turnover time compared to Table 4. This resulted in a reduction of the relative error (cv) of the sum of soil carbon inputs by 3%, 11%, and 0% for Spruce, Pine, and Beech, respectively. For Spruce and Beech, the lifetime of branches became the most important parameter. For Pine, the foliage parameters still had the highest importance index.

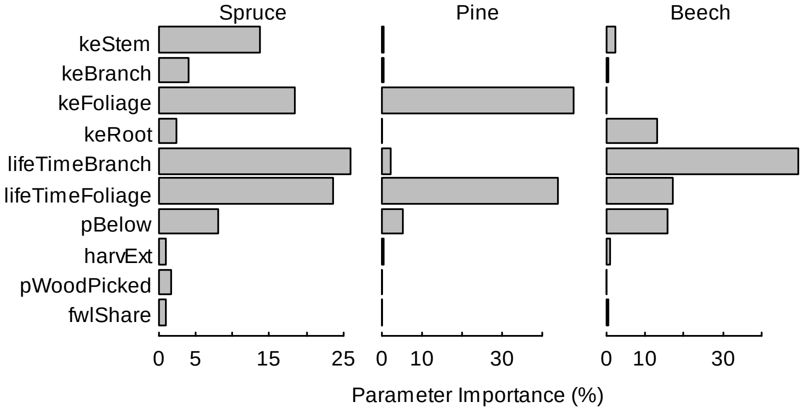
The reliability of the applied model approach is shown by the comparison with field data given in Figure 7. The modeled data well matched the range of measured annual leaf litter fall at for beech study sites.

Discussion

Forest soil carbon inputs by litter production and are usually derived using forest inventories (de Wit et al. 2006, Liski et al. 2006, Ågren et al. 2007). However, in most countries, forest inventories are only available for the very recent past. Therefore, this study presented an alternative approach that is based on yield tables instead of forest inventories. We exemplified the approach by estimating long-term mean past litter production based on yield tables that have been used in Eastern Germany. Further we assessed the uncertainties of the results and the importance of several input parameters.

The litter production by residues from **thinning and harvest** was smaller than the litter production by biomass turnover but of the same magnitude (Fig. 3, Fig 4). Self-thinning did not significantly affect soil carbon inputs in forests of the most common tree species. This can be explained by the fact, that the management proposed in yield tables result in stand densities at which no or only slight competition for light occurs. For Birch, Maple and Pine self-thinning contributed to soil carbon inputs in the same magnitude as harvest residues. However, most of the self-thinning occurred in the period of precommercial thinning, where all wood remains at the site. And soil carbon stocks do not depend much upon whether tree biomass entered the forest floor by self-thinning or as harvest residues. While allocation has been studies extensively before (Burschel et al. 1993, Baritz and Strich 2000, Löwe et al. 2000, Lehtonen et al. 2004a, Levy et al. 2004, Jalkanen et al. 2005, Zianis et al. 2005) and also estimating turnover of leaves and branches has been studied (Lehtonen et al. 2004b, Muukkonen and Lehtonen 2004, Ågren et al. 2007) only minor research has been done to quantify harvest residues. At regional or national scale forest statistics have been used (Ågren et al. 2007). However, it is difficult to use

Figure 6 Importance index, i.e. relative influence of the parameter uncertainty on the results uncertainty, for litter production of intermediate site quality. For all species the mean lifetime of foliage is very important, for Pine also the conversion from timber to foliage biomass. The mean life time of branches is the most important factor for Spruce and Beech. Uncertainty in information on harvest (last three parameters) is not contributing much to the uncertainty in results in all three cases.



regional forest statistics at stand level. Hence, in many studies a fixed portion of stemwood is extracted and the other compartments are left on site. For example Kaipainen et al. (2004): transferred 10–15% of stemwood from the thinnings and the final cuttings to litter. In contrast, the presented study explicitly takes into account first, the distinction between precommercial and commercial thinning (Table 1), second, the age-dependency of the proportion of remaining wood (Fig. 2), and third, self-thinning.

Site quality, as expressed by the site index, had a large influence on both, litter production by biomass turnover and litter production by harvest residues (Fig. 4). The effect of site quality is of the same magnitude as differences by species and as the mean of soil carbon inputs. Published soil carbon studies at the national scale consider age classes and species, but often site quality is not taken into account explicitly (e.g. de Wit et al. 2006, Liski et al. 2006, Ågren et al. 2007). However, our results suggest that site index should be explicitly accounted for.

We used the **Monte-Carlo approach** to study the uncertainty of the calculated soil carbon. An alternative approach would have been error propagation methods. However, error propagation methods assume specific distributions of the parameters and all intermediate results, and they have problems with non-linearity, because they are usually based on a first order Taylor expansion (Winzer 2000). Contrary, Monte Carlo analysis is an effective method to assess uncertainty when models are complex with non-linearity and with different types of correlations (Morgan and Henrion 1990, Vose 1996). When we compare our estimates of litter production of spruce of intermediate site quality (3.8 t/ha/yr) with an estimate across all forests in Finland (Peltoniemi et al. 2006), their estimates are slightly lower (2.7-3.0 tC/ha/yr). This is reasonable, because we expect forests in the region of our study to be more productive. Peltoniemi et al. (2006) also performed an Monte-Carlo analysis and quantified the standard deviation of litter production, i.e. soil carbon inputs, to be 0.36 tC/ha/yr, corresponding to a 13% relative error. Our higher estimate of relative error of 18% is probably because we used a higher uncertainty of foliage turnover. When aggregating the results of a set of stands or strata to a larger forest area, the precision of the aggregated value increases with the square root of the number of stands or strata (Kurth et al. 1994). Smith and Heath (2001) found with an uncertainty analysis of ecosystem carbon stocks, that introducing temporal correlations decreased uncertainty very much. Peltoniemi et al. (2006) demonstrated, that estimating litter from standing biomass overestimates temporal correlation and underestimates uncertainty of annual results. In our study, temporal correlations were not as important, because we aggregated results across an entire rotation period (Eq. 1). In our results, also the inclusion of correlations between model biomass expansion factors of different compartments did not change the distribution of soil carbon inputs significantly (Fig. 5).

The results of the **sensitivity analysis** strongly depend on the assumptions about the distribution of the parameters. We assumed a right-skewed log-normal shape for all parameters. This distribution is more suitable than a normal distribution especially for the conversion factors and the lifetimes of foliage and branches than a normal distribution. On the one side, values below zero, which can occur in the normal distribution, are clearly not valid. On the other side values larger than twice the mean are observed occasionally. However, we expect the shape of the distribution to not affect the distribution of the results very much (e.g. Smith and Heath 2001). For some of the parameters we assigned subjective values. In the Monte-Carlo simulations we therefore assigned rather high relative errors to these parameters in order to reflect our lack of knowledge about theses parameters. However, in the sensitivity analysis, some of these uncertain parameters did not influence the calculated litter production very much (proportion of fine wood in harvest residues, proportion of coarse harvest residues that are collected for private combustion, and to some extent also uncertainty of the ratio of below ground litter production). The importance index reflects both, the uncertainty of the parameter and the sensitivity of the parameter (Hamby 1994). On the one side there are parameters that are uncertain but not sensitive (e.g. collected coarse wood). They are not very important for the uncertainty of the results. On the other side, there are sensitive parameters. Small changes in these parameters have a substantial influence on the results. However, if their precision is high, i.e. they have a low relative error, then they are also not important for the uncertainty in the results. Hence, we should concentrate on the parameters that are important, i.e. sensitive and uncertain.

For all species, the **lifetime of foliage** was a very important parameter (Fig. 6). Mean lifetime is the reciprocal of the turnover. Ågren et al. (2007) found, that the mean lifetime of needles of Spruce and Pine is correlated to latitude.

However, Wachter (1985) found that mean lifetime of spruce needles varied by 13% already at regional scale and that lifetime increased with altitude and water availability. A combined observation and modeling study (Muukkonen and Lehtonen 2004) quantified a range of turnover times of Spruce needles of 0.7 to 0.13 yr^{-1} for southern Finland, which corresponds to a relative error of 15%. Bornkamm et al. (2003) cited 8 studies of pine needles in which a mean lifetime between 2 and 3 years was found in Slovakia, Estonia, southern Finland, England and northern Germany. However, their own measurements in Germany resulted in a mean life time of pine needles of 1.7 years. They attributed this low value to periods of hot and dry weather conditions. Therefore, we used a relative error of 25% for pine, which is considerably higher than the 11% that was used for foliage by Peltoniemi et al. (2006). For broadleaved forests most studies assume a turnover rate of 1 yr^{-1} because all foliage is shed. However, some of the carbon is translocated during leaves senescence or consumed by herbivores before reaching the ground. Fahey et al. (2005) reported 16 to 26% maximum extent of carbon resorption from the differences in leaf area to weight ratio between late-season live foliage and fresh litterfall for northern American hardwood forest. Similar to Fahey's approach, we quantified a value of 9% of carbon resorption from data of a Common beech forest in northern Spain (Regina and Tarazona 2001). Hence, in this study we used a beech foliage carbon turnover rate of 0.9 yr^{-1} instead of 1.0 yr^{-1}. In order to improve precision of soil carbon inputs, environmental dependencies of foliage carbon turnover should be studied further and incorporated into the carbon turnover calculation.

For Beech and Spruce, also the **lifetime of branches** had a substantial influence on litter production (Fig. 6). Because we did not find explicit literature on beech branch turnover, we estimated branch turnover and its error by dividing branch biomass by branch litterfall for each of 16 stands from the study of Mund (2004). The turnover had a large variability (cv=74%) and declined with stand age (r^2=0.52). The correlation between branch turnover and tree diameter was studied for Spruce (Muukkonen and Lehtonen 2004) and Pine (Lehtonen et al. 2004b) in southern Finland. A next step in improving the estimates of soil carbon inputs is to perform similar studies in other regions too, and to implement the derived results in the carbon turnover calculation.

In the following we discuss how and why some aspects of the used **methods differed** from previous studies. Other studies calculated fine root litter production similar as foliage litter production by estimating biomass and turnover (e.g. Peltoniemi et al. 2004). However, both, the estimation of fine root biomass and the turnover is still very uncertain (Matamala et al. 2003, Hutchings and John 2004, Majdi et al. 2005, Godbold et al. 2006, Mulia and Dupraz 2006). Hence, some studies use the idea of functional scaling, which suggests a stable proportion between foliage and root biomass, to estimate fineroot biomass (Vanninen and Makela 1999, de Wit et al. 2006). However, with this approach there is still the uncertainty of fineroot turnover. Therefore, we followed an approach of Ågren et al. (2007), which extends the idea of functional scaling to litter production. Hence, we use a fixed ratio of below ground litter production to above ground litter production. Our study, as well as previous studies, did not distinguish between soil carbon inputs by fine root litter production and by root exudates. However, evidence is accumulating that the carbon transport by root exudates is a major carbon flux with a different dynamics in soil (Fahey et al. 2005, Högberg and Read 2006).

Two important factors were not taken into account explicity in this study. These are ground vegetation and natural disturbances. Peltoniemi et al. (2006) applied a mean biomass stock of ground vegetation of 3.8 t/ha and a mean turnover rate of 0.33 yr^{-1} based on more detailed data for forests in southern Finland (Peltoniemi et al. 2004). Application of the same numbers together

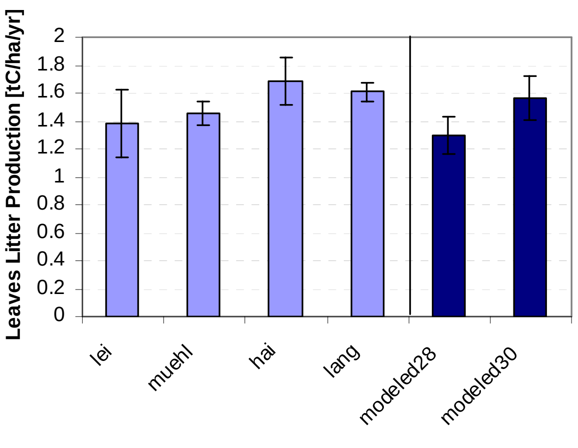


Figure 7 Comparison of calculated litter production by leaves for beech with litter fall data from Mund (2004). Both, the mean and the standard deviation (error bars) of values calculated for two site indices 28m and 30m (two dark right columns) well match the range of carbon in measured litter fall.

with 50% carbon content to this study would lead to an additional increase of non woody litter production of 0.63 tC/ha/yr. A part of the natural disturbances is accounted for by the yield tables, which state that only 80% of the given basal area should be thinned. The other 20% of the thinned basal area will be killed due to other reasons such as disturbance (Wenk et al. 1985). However, if there are larger scale disturbances, litter production will be larger compared to the values presented in this study.

The good agreement between **calculated and measured leaf litter production** (Fig. 7) increases our confidence in the calculated soil carbon inputs. While the sites Leinefele (lei) and Muehlhausen (muehl) have been managed according to yield tables, the Hainich site (hai) represents an unmanaged forest and the Langula site (lang) a selection cutting system. However, leaf litterfall is estimated quite well for all the sites with the yield table based approach showing that the uncertainty of the modelled values are in the range of the variability caused by the studied management activities.

Conclusions

- Residues left after thinning and harvest contributed to litter production in the same magnitude as the continuous biomass turnover. Therefore, it is important to consider at least one full rotation period including thinning operations and final harvest for estimating long-term mean litter production.
- Both, different species and differences in site quality for the same species caused variability in litter production that was of the same magnitude as the mean of litter production. Hence, site quality is very important for estimating litter production at stand scale, but should also be taken into account at broader scales.
- We quantified the relative error of the presented litter production to be 14%, 17%, and 25% for Beech, Spruce, and Pine stands respectively. This uncertainty was mainly due to the large natural variability in foliage biomass and foliage lifetime. A better explanation of this variability by environmental conditions will improve the precision.
- Long-term means of past litter production rates and their uncertainty can be reliably estimated for the former century on the basis of yield tables. The presented approach can provide a new tool to establish the baseline carbon stocks in dynamic soil carbon models (Peltoniemi et al. 2007, Wutzler and Reichstein 2007), which in turn can be used for soil carbon monitoring.

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Soils apart from equilibrium - consequences for soil carbon balance modelling

Abstract Many projections of the soil carbon sink or source are based on kinetically defined carbon pool models. Parameters of these models are often determined in a way that the steady state of the model matches observed carbon stocks. The underlying simplifying assumption is that observed carbon stocks are near equilibrium. This assumption is challenged by observations of very old soils that do still accumulate carbon. In this modelling study we explored the consequences of the case where soils are apart from equilibrium. Calculation of equilibrium states of soils that are currently accumulating small amounts of carbon were performed using the Yasso model. It was found that already very small current accumulation rates cause big changes in theoretical equilibrium stocks, which can virtually approach infinity. We conclude that soils that have been disturbed several centuries ago are not in equilibrium but in a transient state because of the slowly ongoing accumulation of the slowest pool. A first consequence is that model calibrations to current carbon stocks that assume equilibrium state, overestimate the decay rate of the slowest pool. A second consequence is that spin-up runs (simulations until equilibrium) overestimate stocks of recently disturbed sites. In order to account for these consequences, we propose a transient correction. This correction prescribes a lower decay rate of the slowest pool and accounts for disturbances in the past by decreasing the spin-up-run predicted stocks to match an independent estimate of current soil carbon stocks. Application of this transient correction at a Central European beech forest site with a typical disturbance history resulted in an additional carbon fixation of 5.7±1.5 tC/ha within 100 years. Carbon storage capacity of disturbed forest soils is potentially much higher than currently assumed. Simulations that do not adequately account for the transient state of soil carbon stocks neglect a considerable amount of current carbon accumulation.

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Introduction

The widely applied soil carbon models Century (e.g. Parton et al. 1988), Roth-C (Jenkinson 1990), Romul (Chertov et al. 2001), Yasso (Liski et al. 2005) and many other models are based on kinetically defined pools. This means, that decomposition is described by removing a constant fraction of a pool at each time step. This fraction, which distinguishes the pools, is called the decay rate or decomposition rate. It is often modeled with a dependence on environmental conditions, in most cases temperature and moisture. Despite simplifying many soil processes, these models have proven to predict reasonable soil carbon stock changes during decadal time scales (e.g. Smith et al. 1997). However, there is a controversy whether the decay rates of the slower (more stable) pools have a lower, equal or higher dependence to warming than the faster pool (Ågren 2000, Davidson and Janssens 2006). The different answers to this question cause large differences in the long term soil carbon sink or source. While the decay rates of the faster pools have been determined by experimental results, the decay rates of the slower pools have been calibrated in a way that a models steady states matches observed carbon stocks (e.g. Liski et al. 2005). The underlying assumption is that the observed carbon stocks represent equilibrium stocks. This assumption also allows a determination of the initial state of the model for given constant average inputs and parameters by simulating the model until an equilibrium state is reached (spin-up-runs) (e.g. Smith et al. 2005). However, observed soils might be far away from equilibrium because of possible very long turnover times of stable compounds and disturbances by fire, erosion, land use or land use change. The equilibrium assumption is challenged by observations of steadily increasing carbon stocks of very old soils. Wardle *et al.* (1997) observed carbon stocks of about 240 tC/ha in the organic layer on small islands in northern Sweden, where fire was prevented. Sizes of the stocks correlate with the time since last disturbance (1000 to 3000 years). This implies increasing stocks at old soils. Many modellers argue that the

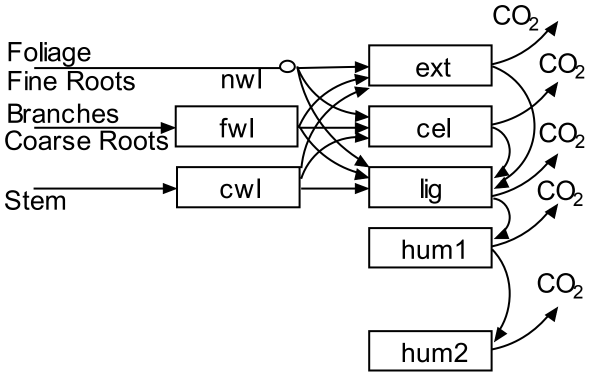


Figure 1: Model Structure of the Yasso Model (Liski et al. 2005). The pools on the left side describe woody litter that becomes available for decomposition after a delay (nwl: non-woody litter, fwl: fine woody litter, cwl: coarse woody litter). The pools on the right side (ext: extractives, cel: celluloses, lig: lignin, hum1: humus1, hum2: humus2) represent soil carbon pools of different stability that are modeled by different decay rates of an exponential decay. The ext pool has the largest decay rate (i.e. least stability and shortest turnover time) and the hum2 pool has the smallest decay rate (i.e. highest stability and longest turnover time).

equilibrium assumption might be wrong, but it works and must be used until other approaches are evolving. Nevertheless, the consequences of relaxing the equilibrium assumptions are not well understood.

The aim of this study was to explore the consequences of a relaxed equilibrium assumption. The paper has the following outline. In a first part we perform an equilibrium experiment using the Yasso model's standard parameterization and show that the decay rate of the slowest pool and theoretical equilibrium stocks are highly uncertain. This implies that soil might be far apart from theoretical equilibrium yet. Based on these findings we propose a method how to initialize models to a transient state instead of equilibrium. In a second part we apply this initialization to a Central European case study. We discuss consequences for current soil modelling. Further, we show and discuss ways to overcome the equilibrium assumption.

Methods

The Yasso model

The soil carbon model Yasso was designed by Liski et al. (2005) in order to model soil carbon stocks of mineral soils in managed forests. Despite its simplicity and low demands on input data and parameters it shares many properties of the family of models that are based on kinetically defined pools. Figure 1 displays the model structure and the flow of carbon. The right part describes the separation of the different litter types into compartments that correspond to the kinetically defined pools and it describes a delay of the woody litter compartments before decomposers can attack the chemical compounds. The left part describes the decomposition of the chemical compounds. The decay rates are dependent on mean annual temperature (or alternatively effective temperature sum) and a drought index (difference between precipitation and potential evapotranspiration during vegetation period). In the standard parameterization the decay rates of the slower pools are less sensitive to temperature increase than the fast pools (hums one: 60%, humus two: 36% of sensitivity of fast pools). The model has been tested and successfully applied to boreal forest (Peltoniemi et al. 2004), litter bag studies in Canada (Palosuo et al. 2005), and as part of the CO2FIX model all over Europe (e.g. Nabuurs and Schelhaas 2002, Kaipainen et al. 2004).

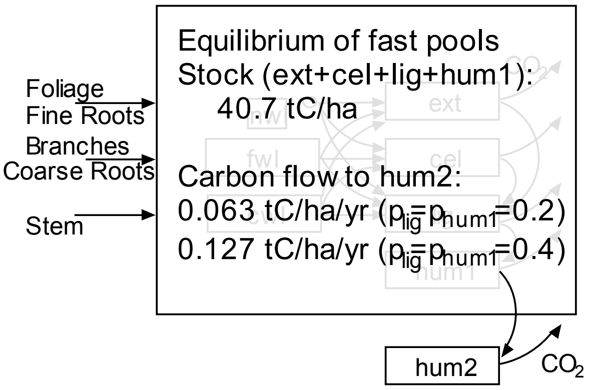


Figure 2: Relaxed equilibrium assumption: All pools are assumed to be in equilibrium except the slowest pool (hum2). Constant average litter input determines equilibrium stocks of the faster pools and the constant flow to the slowest pool.

The relaxed equilibrium assumption

The relaxed equilibrium assumption corresponded to the usual equilibrium assumption, except that the slowest pool was excluded from this assumption. Assuming that time since last disturbance is longer than a century and that the inputs to the soil system did not change much within this time, the faster pools (turnover times of at most decadal time scale) have had enough time to recover from former disturbance. They were regarded to be near a dynamic equilibrium (averaging across changes during rotation periods and with climate fluctuations). The relaxed equilibrium assumption assumed that this is not true for the slowest pool which needs long time scales to reach the theoretical equilibrium. Hence the relaxed equilibrium assumption assumed the slowest pool to be still accumulating (Table 1). If all the faster pools are in equilibrium, the input rate to the slowest pool is constant (Fig. 2).

Table 1: Comparison of equations between the usual equilibrium assumption and the relaxed equilibrium assumption for the slowest pool. *k*: decay rate, *i*: input rate, C_c: current stock, C_e: equilibrium stock.

	Usual	Relaxed
Equilibrium stock	$C_e = \frac{i}{k} = C_C$	$C_e = \frac{i}{k} > C_C$
Mass balance	$i = k \cdot C_c$; $\frac{\delta C_c}{\delta t} = 0$	$i = k \cdot C_c + \frac{\delta C_c}{\delta t}$
Decay rate	$k = \frac{i}{C_c}$	$k = \frac{i - \frac{\delta C_c}{\delta t}}{C_c}$

The equilibrium experiment

Using this relaxed equilibrium assumption we determined the decay rates of the slowest pool of soils that are recovering from former disturbance. The development of the carbon stock of the slowest pool *C* (tC/ha) over time *t* (yr) was described by a first order kinetics with decay rate *k* (1/yr) and with input *i* (tC/ha/yr) (Eq. (1)).

$$\frac{\delta C}{\delta t} = i - k \cdot C \tag{1}$$

When applying a constant input rate, integration of equation (1) resulted in the closed form of Eq. (2), where *a* (dimensionless) is an integration constant.

$$C = \frac{i}{k}\left(1 - ae^{-k \cdot t}\right) \tag{2}$$

Constraining the stock at time *t*=0 to C_0 in Eq. (2) gives Eq. (3).

$$C = \frac{i}{k} - \left(\frac{i}{k} - C_0\right) \cdot e^{-k \cdot t} \tag{3}$$

The decay rate *k* can be expressed as a function of the current stock C_c, (tC/ha), input *i*, and by an approximation of its current rate of assimilation $\frac{\Delta C_c}{\Delta t}$ (tC/ha/yr). Resolving Eq. (1) for the decay rate gives Eq. (4).

$$k = \frac{i - \frac{\Delta C_c}{\Delta t}}{C_c} \tag{4}$$

For a given decay rate *k*, the equilibrium stock, which corresponds to an assimilation rate of 0, is given by Eq. (5).

$$C_e = \frac{i}{k} \tag{5}$$

And the accumulation time t_{95} (yr), i.e. the time for an increase of stocks from zero to 95% of equilibrium stock, is given by Eq. (6).

$$t_{95} = \frac{\ln(0.05 \cdot C_e)}{k} \tag{6}$$

In the equilibrium experiment we prescribed different current assimilation rates and calculated corresponding decay rates of the slowest pool (Eq. (4)). Given these decay rates, we determined equilibrium stocks (Eq. (5)), and the times that are needed to accumulate 95% of these stocks (Eq. (6)). Initial pools size (40.7 t/ha) and input to the slowest pool (i=0.063 tC/ha/yr) were calculated by equilibrium of the faster pools of the Yasso model with standard parameterization for Norway spruce in standard climate (Appendix B). Reasonable constant average litter inputs of Norway spruce were applied (non woody litter=1.7 tC/ha/yr, fine woody litter=1.4 tC/ha/yr, thin coarse woody litter=0.1 tC/ha/yr, large coarse woody litter=0.1 tC/ha/yr). The development of carbon stocks with average litter inputs represents the trend (moving average over time) of the carbon stocks that result from the application of non-constant litter input. Additionally, calculations were repeated using an increased input to the slow pool (i=0.127 tC/ha/yr) that resulted from a change in the Yasso parameterization in which a larger part of decay material was spent to form more recalcitrant compounds (p_{lig}=p_{hum1}=0.4).

The transient correction

In continuation to the results of the equilibrium experiment, we developed a method of correcting spin-up-run predicted pool sizes for the effects of former disturbance. This “transient correction” is only valid for sites that have not been disturbed for about a century, because it uses the relaxed equilibrium assumption, which assumes that all pools are in equilibrium except the slowest pool. According to the results of the equilibrium experiment, which are described in the results section of this study, the effects of former disturbance are an overestimation of the slowest pool’s decay rate in model calibration and that current carbon stocks are smaller than equilibrium carbon stocks. Hence, the correction, first, prescribes a lower decay rate of the slowest pool. Below it will be shown that about 20% of the decay rate that is determined by the usual equilibrium assumption is appropriate for century term simulations. Second, the correction decreases

Table 2: Scenario groups of the simulations of the Leinefelde/Mühlhausen chronosequence. Within each group simulations were performed with different decay rates of the slowest pool (hum2) and repeated with increase temperature sensitivity.

Scenario Group	Description
base	current inputs and current temperature
litter	increase of litter inputs by assuming that all the wood remains in the forest (conservation scenario)
t3-t9	increase of temperature by 3,6, and 9 Kelvin gradually over the next 100 years
t3+litter	increase of litter input and increase of temperature by 3 Kelvin

Table 3: Average litter inputs to the Yasso model [tC/ha/yr]. nwl: non woody litter, fwl: fine woody litter, cwl_small: coarse woody litter with a diameter diameter 6-20cm, cwl_large: coarse woody litter with a diameter 20-60cm.

Scenario Group	nwl	fwl	cwl_small	cwl_large
base, t3-t9	3.15	0.53	0.21	0.085
litter, t3+litter	3.15	0.87	1.24	0.214

the spin-up-run predicted equilibrium stock of the slowest pool by subtracting an amount of carbon. The amount that has to be subtracted is chosen so that the sum of the stocks of the soil carbon pools matches an independent estimate of current carbon stocks.

Application of the transient correction

In order to test the performance of the transient correction, we applied the transient correction at a Central European beech forest chronosequence (Mühlhausen/Leinefelde). The sites of the chronosequence have been managed as a shelterwood system. In the EU-project FORCAST, litter fall, organic layer carbon stocks, and soil carbon stocks have been measured (Mund 2004). Carbon pools of the soil model were initialized with spin up runs with constant average litter inputs and climatic conditions (mean average temperature: 6.8°C, drought index: 71.3mm). All sites of the chronosequence have been disturbed by wood pasture about 150 years ago and some sites have been possibly used as agricultural land before the 16th century. The several sites of the chronosequence represent different stand ages of the one simulated site. As independent estimate of soil carbon stocks for the transient correction the sum of the measured carbon stocks of the mineral soil (41.7±5.0 tC/ha) and the organic layer (3.7±0.8 tC/ha) was used. The used standard parameterization of the Yasso model is listed in Appendix B.

We studied the effect of assuming different intrinsic decay rate of the hum2 pool (slowest most stable pool of the Yasso model) on both, the average carbon stock, and the uncertainty of the carbon stocks after 100 years. The decay rate was varied by dividing the standard value of 1.2e-3 yr^{-1} by 1, 5, 25, 125, and 625. This corresponds to turnover times of 830 to 5.2e5 years. We used four scenario groups in order to gain insight, in how this effect varies with combinations of changes in temperature and litter input (Table 2). Table 3 lists average litter inputs to the Yasso model. We did not vary litter inputs with stand age but applied a constant litter input that was averaged across one rotation cycle. For details of derivation of litter input see Appendix A. First we studied the effect with four scenario groups and standard parameterization. Next, we studied the effect in four scenario groups that differed from the corresponding previous scenario groups by increased temperature sensitivity of the slow pools apparent decay rate. The apparent decay rate depends on the intrinsic decay rate, water availability, temperature, and several parameters. We modified the standard parameterization in a way so that the slowest pools were as sensitive to warming as the decay rates of fast pools (s1=s2=100%).

Results

Decay rates and equilibrium stocks in the equilibrium experiment

Current carbon stocks can be explained by different decay rates of the slowest pool if the equilibrium stock is not fixed (Fig. 3). The difference between the trajectories of carbon stocks with different decay rates within a few years is very small (<10 g/ha/yr). However, the assumption of already very small current accumulation rates in the equilibrium experiment resulted in profound changes of equilibrium stocks. We calculated (Eq. 4-6) large changes in the resulting decay rate (Fig 4a), in the theoretical equilibrium stocks (Fig 4b) and the accumulation times (Fig. 4c). This is explained as follows. If the assumed rate of change was approaching the input rate to the slowest pool, the difference between input and accumulation approached zero. Hence, the decay rate also approached zero (Fig 4a). This caused the equilibrium stocks and the times to reach these stocks to approach infinity. The limit

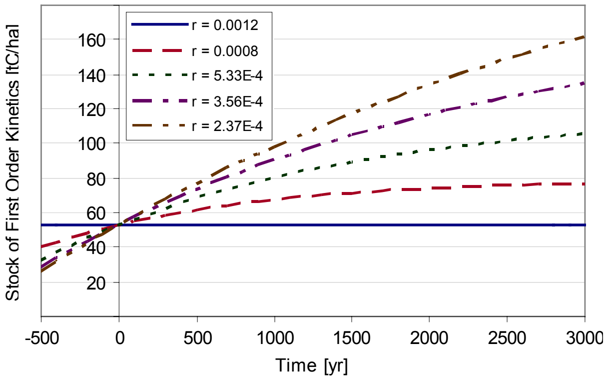


Figure 3: Trajectories of the slowest pool of the Yasso model with different decay rates. Dynamics is described by a first order kinetics with constant input (Eq. (3)): $C = \frac{i}{k} - \left(\frac{i}{k} - C_0\right) \cdot e^{-k \cdot t}$; input i = 0.06345 tC/ha/yr; stock at time zero C0 = 52.874 tC/ha. At time t=0 the current carbon stock C0 is observed. The lower the decay rate, the larger is the current rate of carbon accumulation, which is given by the slope ΔC/Δt at time zero.

case, when the rate of change was equal to the input, corresponded to an inert pool that is not decomposed. With doubling the proportion of carbon that is used to form more recalcitrant components $p_{lig}=p_{hum1}=0.4$, the limit case had a different position. However, despite this big change to the model, the pattern was the same. With the assumption of small current accumulation rates decomposition rates were much lower (Fig. 4a cross symbols) than without a current carbon accumulation and theoretical equilibrium stocks were much higher (Fig. 4c cross symbols).

Effects of accounting for former disturbance by the application of the transient correction

The sum of the equilibrium carbon pools after the spin-up-run exceeded observed stocks by about 30% for the Mühlhausen/Leinefelde study site that has been disturbed until 150 years ago (Fig. 5).

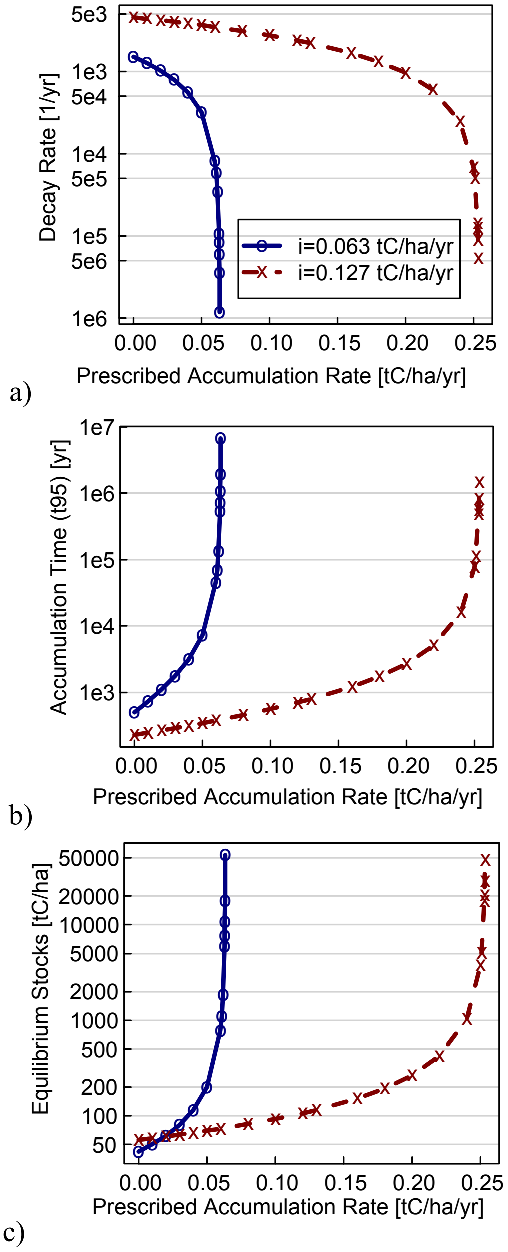
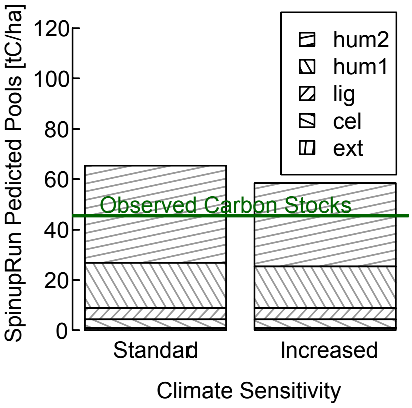


Figure 4: Decay rates (a) (Eq. (4)), equilibrium stocks (b) (Eq. (5)), and accumulation times (c) (Eq. (6)) that result when different rates of current carbon accumulation (x-axis) are prescribed. Symbols correspond to two different equilibrium inputs that result from a variation in the proportion of decomposed mass in the Yasso Model.

Figure 5: Transient correction at the Mühlhausen/Leinefelde site. Spin-up-runs of the Yasso model simulate the theoretical equilibrium stocks of the kinetically defined soil carbon pools (ext, cel, lig, hum1, and hum2). The transient correction decreased the slowest pool (hum2) so that the sum of the pools matches the observed carbon stocks. Climatic sensitivity: The decay rates of the slower pools were less sensitive to warming than the faster pools with standard parameterization and equally sensitive (s1=s2=100%) in the scenarios of increased temperature sensitivity.



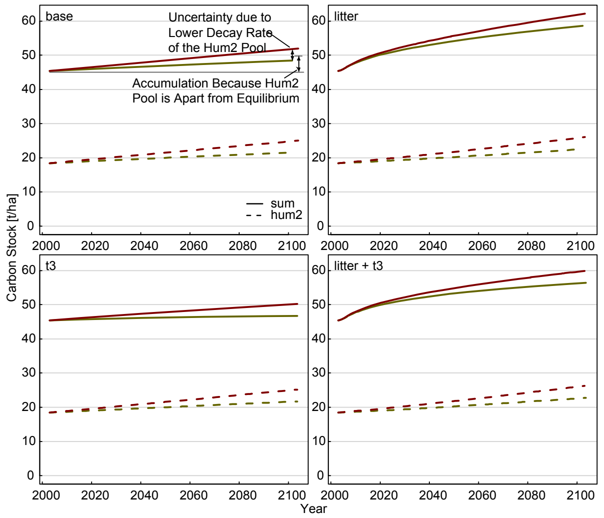


Figure 6: Development of the soil carbon stocks at the Leinefelde chronosequence simulated by the Yasso model with standard temperature sensitivity. *sum* represent the sum of the stocks of the Yasso soil pools (ext+cel+lig+hum1+hum2). The lower ones of the diverging lines are trajectories of the simulation with standard parameterization of the slowest pool decay (k_{hum2} = 1.20e-3) and upper ones of a much lower value (k_{hum2} = 1.92e-06). The four panels correspond to different scenario groups (base: no change in litter inputs and temperature, litter: increase litter input, t3: temperature increase of 3K gradually over 100 years).

With the relaxed equilibrium assumption (all pools are in equilibrium except the slowest pool), we interpreted that the slowest pool (hum2) was far from equilibrium yet. The application of the transient correction decreased the slowest pool, i.e. the carbon above the line of observed carbon stocks in Fig. 5. In the scenario of increased temperature sensitivity the relative proportion of the slowest pool after the correction was larger because the spin-up-runs resulted in smaller sum of stocks of all the pools.

The carbon accumulation due to the adjustment of the spin-up-run predicted pools for former disturbances was 5.7±1.5 tC/ha with standard temperature sensitivity (Fig. 6 top left) and 5.5±1.8 tC/ha with increased temperature sensitivity (Fig. 7 top left) within 100 years for the baseline scenario. This corresponds to a flux of 5.7gC/m²/yr and an increase of about 13% of initial carbon stocks over 100 years. This carbon accumulation would have been neglected without the transient correction. The transient correction prescribes a lower intrinsic decay rate of the slowest pool but does not specify this rate. Hence, we studied the uncertainty that resulted from a range of prescribed decay rates that correspond to turnover times from 830 to 5.2e5 years. The absolute amount of uncertainty of 1.5 tC/ha (or 1.8 tC/ha for increased slow pool temperature sensitivity) did not change much with different scenarios of litter input and temperature increase (Fig. 6 and 7). Hence the relative size of the uncertainty depended on the projected change of carbon stocks and varied between 9% in the conservation scenario (Fig. 7 litter) and 59% in the temperature increase scenario (Fig. 7 t3).

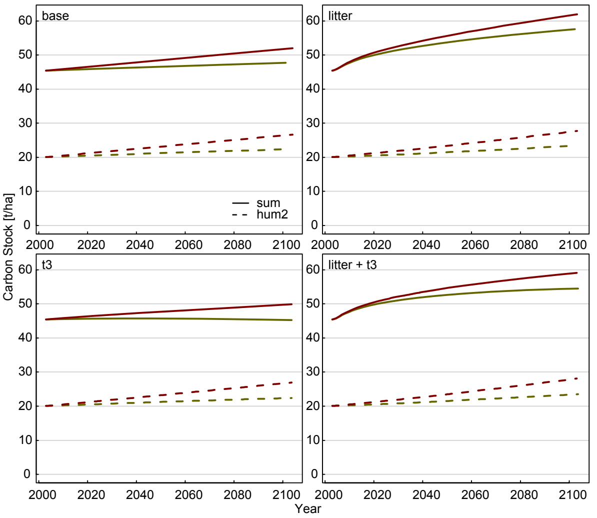


Figure 7: Development of the soil carbon stocks at the Leinefelde chronosequence simulated like the ones in figure 6 except an increased temperature sensitivity of the slow pools (*s1*=*s2*=100%).

Assuming lower decay rates of the slowest pool resulted in an increased carbon accumulation (Fig. 8). Consistently across all scenario groups, the carbon accumulation increased most with the first decrease of the slowest pool's (hum2) decay rate to 20% of standard parameterization. Further decrease of the decay rate to 4%, 0.8%, and 0.16% of standard parameterization only slightly increased carbon accumulation during 100 years.

Discussion

Highly uncertain decay rates and equilibrium stocks

Our study for the first times explores the consequences of relaxing the usual assumption that soil carbons stocks are in equilibrium. The consequences for the parameterization of slow pool decay rates and resulting theoretical long-term equilibrium were studied by performing an equilibrium experiment, in which the slowest pool was still accumulating carbon. The equilibrium experiment showed that already very small rates of current accumulation caused tremendous changes in equilibrium stocks (Fig. 4). The necessary accumulation rates are so small, that it is practically impossible to measure them within a few years. The times to reach equilibrium could span millennia. Hence, soils may be far apart from a theoretical equilibrium. The theoretical equilibrium does not account for non-respiratory losses out of the system. Hence, soils may never reach this theoretical equilibrium because of changing conditions and partial resets by disturbances (e.g. forest fires (Parker et al. 2001, Wardle et al. 2003), or erosion (Hedges et al. 1997, Polyakov and Lal 2004)). In addition soil weathering continues and soil horizons may change in a way to increase humus stabilization and potential carbon stocks.

The transient correction – an approach to account for former disturbance

In order to account for **account for former disturbances**, we suggested a heuristic technique that we call the transient correction. Soils that have been disturbed centuries ago are still in a transient state due to the long timescales of the slowest pool. The transient correction can account for this transient state, where the relaxed equilibrium assumption is valid (time since last disturbance is longer than a century).

The transient correction does not specify the decay rate of the slowest pool, because the rate can not be determined by calibrating equilibrium states to current stocks or observing current stock changes. If no method of constraining this rate is available, 1/5 of the standard decay is a reasonable first estimate, because lower rates did not change results much in decadal time scale, as we showed in our sensitivity analysis (Fig. 8).

The transient correction modifies a valid state by changing the stock of a single pool. This procedure potentially may initialize models to **non-valid states**. However, most models have no feedbacks or very weak feedbacks from the slowest pool to the other pools. Hence, we do not expect big numerical errors or anomalies due to the transient correction when simulating the system.

One precondition for applying the transient correction is an **independent estimate of current soil carbon stocks**. This estimate must account for the disturbance history. Best choice is measuring carbon stocks at the site. However, this is laborious and expensive. If the disturbance history can be assumed to be similar within a region, a spatial extrapolation of measured carbon stocks can be used (e.g. Liski and Westman 1997, Perruchoud et al. 2000, Wirth et al. 2004, Wutzler et al. 2006).

We note, that neither the equilibrium nor the relaxed equilibrium assumption is applicable for sites with more recent (less than a century ago) disturbances. In order to initialize the model for such sites, the stocks of all the pools have to be estimated. There are recent advances in reflectance methods to achieve this (Couteaux et al. 2003). Zimmermann et al.(2006) related fractions of grassland soil carbon that were distinguished chemically to the carbon pools used in the Roth-C model. These pools then could be classified quite well by analyzing reflectance spectra.

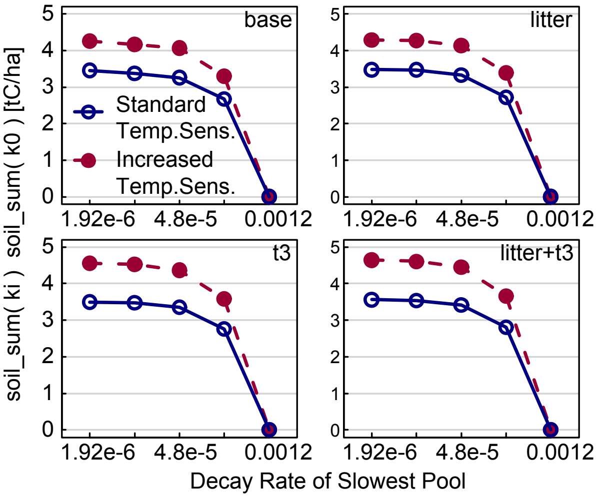


Figure 8: Difference of carbon stocks from base line (standard parameterization, khum2=0.0012) after 100 years (y-axis) caused by different parameterization of the decay rate of the slowest pool (logarithmic x-axis). The four panels correspond to different scenario groups (base: no change, litter: increase litter input, t3: increased temperature).

Incorrect initial model state and underestimation of carbon accumulation and it's uncertainty

Previous model studies of soil carbon stock changes (e.g. Liski et al. 2002) did not take detailed account for the effect of soils recovering from former disturbance. We exemplified the consequences of relaxing the equilibrium assumption on development of soil carbon by applying the transient correction together with the YASSO model to a Central European beech forest.

If soils are apart from equilibrium, this leads to a big overestimation of the decay rate of the slowest pool with the current method of constraining the slow pool decay rates. The spin-up-runs will still give reasonable results for soils that have a similar disturbance history as the sites used for parameterization of the model (Peltoniemi et al. 2004). However, with an overestimated decay rate of the slowest pool, the spin-up-runs underestimate the stock at sites that have not been disturbed for a very long time. Further it overestimate the stock at sites that have been disturbed in the last two or three centuries ago. For this time we can assume that the sites used for parameterization of the Yasso model have not been severely disturbed. The spinup-runs possibly will overestimate stock at sites where last disturbance is even longer ago, but this depends on disturbance history of the sites used for parameterization of the Yasso model.

When applying the transient correction to the Central European beech forest we found an additional increase due to recovering from disturbance was with 5.7 g/m²/yr (Fig. 6). This additional increase was of the same magnitude as the increase due to climate change projected for Finland (9 g/m²/yr) (Liski et al. 2006) or Sweden (7.5 g/m²/yr) (Ågren et al. 2007). In a first very rough extrapolation to European scale we assume that half of the forested area in Europe is still recovering from former disturbance and that the additional increase that we calculated for the Leinefelde site would occur on this area. With these assumptions, the projected forest soil carbon sink of 7.5 TgC for Europe (EU15 + Norway + Switzerland: 120 million ha) by a recent LPJ modelling study by ATEAM (Lindner et al. 2004, Schröter et al. 2004) would be increased by 3.42 TgC or by 46%. Hence, the potential carbons sink due to recovering from former disturbance is in the same magnitude as the currently projected sink in Europe.

Relaxing the equilibrium assumption added another degree of **uncertainty to projections of carbon stocks**. With applying the transient correction, this additional uncertainty entered the model by the unknown slowest pools decay rate. The uncertainty of projected carbon stocks was smaller than projected stock change but of the same magnitude (Figures 6 and 7). Further, the uncertainty varied with assumptions about the temperature sensitivity of the slow pools decay rates (Fig. 8). This variation of the uncertainty of carbon stock changes was caused in part by the higher initial percentage of the slow pool in the increased temperature sensitivity scenarios (Fig. 5). We suppose that uncertainty of stock changes due to slow pool parameterization will be largest in soils, where the initial percentage of the slow pool after the transient correction is large or where decay rates are high.

Consequences apply also to other models

The models Century (e.g. Parton et al. 1988), Coup (Jansson and Karlberg 2004), Romul (Chertov et al. 2001), RothC (Jenkinson 1990), and the soil model of Biome-BGC (Thornton 1998) all define a very slow pool. Except Romul, which provides a database of compiled initial states, all these models use the equilibrium assumption to infer initial states. Therefore, the consequences of Yasso model simulations also apply to these models. The transient correction should also be readily applicable to these models except the RothC model. The RothC shares the same problem; however the application of the transient correction is impaired. This is because the model specifies no input to the inert pool and already calibrates the size of the inert pool in a way to match average age of soil carbon that was determined by C14 measurements (Martel and Paul 1974, Falloon et al. 1998, Rumpel et al. 2002).

Evidence and tests for the hypothesis of soil carbon stock being apart from equilibrium

From repeated measurement after 5-10 years, we can practically not infer if a soil carbon stock is near equilibrium because small changes in carbon stocks could be attributed to inter-annual variance (Fig. 3). However, the influence of former disturbances, namely former land use, on current soil carbon stocks, C:N ratios, nitrification and other soil properties is confirmed by many studies at several sites (e.g. Koerner et al. 1997, Wardle et al. 1997, Goodale and Aber 2001, Berger et al. 2002, Rothe et al. 2002, Thornton et al. 2002, Mund 2004, Mund and Schulze 2005). These influences can be much stronger than climatic influences (Caspersen et al. 2000, Janssens et al. 2001) and can be observed after 1700 years (Dupouey et al. 2002). A recent review regarding soil carbon changes in forests concludes that the vast intensive cultivation throughout Europe (deforestation, drainage, deflation and erosion) has caused immense historical losses of soil carbon. Nowadays forested areas with degraded soils are abundant and offer a tremendous potential to restore carbon stocks (Baritz et al. 2004). Foster *et al.* (2003) describe processes that alter soil properties in historic timescales. The most important ones are probably tillage (Wall and Hytonen 2005, Grandy and Robertson 2006) and erosion (Polyakov and Lal 2004). Hence, we support the hypothesis that soil carbon stocks of many sites are apart from equilibrium. In order to further increase the evidence we suggest testing some consequences of the hypothesis.

One consequence is the underestimation of current soil carbon stocks for sites that have not been disturbed for a much longer time than the sites used for parameterization. Are these overestimations observed? We did not apply the Yasso model to the old-growth forest with high carbon stocks (Wardle et al. 1997, Harmon et al.

2004), but we realize that the litter input and adjustment of decay rates with climate would not be sufficient to simulate the large observed stocks. Soils with an even longer track (i.e. more than millennia) of stable conditions can be found at sites of tropical evergreen rainforests. However, caution has to be applied in translating models and parameters between boreal and temperate zone. Due to the very different apparent decay rates, the soil carbon stocks are not readily comparable between the temperate and the boreal zone.

A second consequence is the overestimation of current soil carbon stocks for sites that have been disturbed in the last two or three centuries ago. In this study we presented simulations of forest soils that have been disturbed by wood pasture 150 years ago with lower observed carbon stocks than stocks predicted by spin-up runs (Fig. 5). These observations confirm the notion of soils being apart from equilibrium.

Koerner *et al.* (1999) found that $\delta^{15}N$ values increase with intensity of former land use. They related this to former input of ^{15}N enriched manure, and to the activation of soil nitrification. The increase $\delta^{15}N$ can be used as a (yet non-quantitative) tracer of previous land use in forests.

How can we interpret and constrain the slow pool's decay rate without assuming equilibrium?

Currently quite contrasting concepts are existing about which factors processes determine the slow kinetically defined pools and their decay rate, where the biochemical properties of the decaying material (Couteaux et al. 1995, Berg and McClaugherty 2003), physico-chemical stabilization (Mikutta et al. 2006, von Lützow et al. 2006) and microbial limitations of energy and nutrients (Fontaine and Barot 2005) are mentioned as limiting factors. Couteaux *et al.* (1995) present a conceptual model of decomposition in the organic layer that is divided in three phases. The initial phase could be roughly attributed to the decay of the extractives, celluloses, and lignin pools of the Yasso model, the late phase to the pools lignin and humus one pool, and the final stage to the decay of the most recalcitrant pool. Howard *et al.* (1974) found, when extrapolating mass loss of litter bag studies with an asymptotic model, that in many cases the proportion of mass that is decayed, is smaller than 100% and that there is a part of the litter that is transformed to stable components. Berg *et al.* (1996, 2003) termed the asymptote of the decay "limit value" and showed that it can be correlated with litter quality and climatic conditions. If pools are attributed to the decay phases as described above, the portion above the limit value, i.e. the not or extremely slowly decomposing fraction, corresponds to the flux into the slowest pool. It needs to be investigated, if this approach together the age of soil carbon (Martel and Paul 1974, Falloon et al. 1998, Rumpel et al. 2002)can be used to constrain the slower pools without the equilibrium assumption. The parameterization of the slow pools then will depend on litter quality, namely initial nitrogen content, and climatic drivers.

Decomposition, especially the late states, also depends on soil mineralogy and spatial inaccessibility of carbon (Mikutta et al. 2006, von Lützow et al. 2006). Finally, Fontaine and Barot (2005) could increase dramatically the decay rates of the soil organic matter by increasing the energy input into the soil, indicating that microbial starvation could also be a reason for stabilization, particularly in deeper horizons. The YASSO model, however, assumes that decomposition is governed by chemical litter quality and climatic drivers. Hence, the transient correction should only be considered as a diagnostic approach and we believe that models need to be developed which explicitly represent these additional processes give better mechanistic constraints on and interpretation of soil organic matter decomposition rates.

Conclusions

- Observations of current soil carbon stocks are not sufficient to constrain the decay rates of the recalcitrant components and the corresponding equilibrium carbon stocks. The reason is that because of the long time scales of recovering from disturbances it is not known whether carbon stocks are in equilibrium.
- If soils are apart from equilibrium, spin-up runs are only valid for sites that have a similar disturbance history as the sites used for model calibration. The spin-up runs underestimate the stock of sites that have not been disturbed for a very long time, i.e. thousands of year, and overestimate the stock of sites that have been disturbed in the last two or three centuries
- Carbon stocks that have been generated by spin-up runs of models that work similar as YASSO should be corrected by the "transient correction". This means to adjust the slowest pool in a way that the sum of soil pools matches an independent estimate of soil carbon stocks. Such an estimate can be obtained by soil carbon stock observations or by regional

statistical models that can account for the unknown but similar disturbance history.

- In century-term simulations the uncertainty due to the unknown decay rate of the slowest pool results in uncertainty of stock changes in the magnitude of 1’ g/m^2/yr. This considerable amount of uncertainty is of the same magnitude of the simulated changes in soil carbon stocks due to litter input and climate change. The amount of uncertainty does not change very much with changing litter input and changing temperature. However, this amount increases with temperature sensitivity of the slow pools and the initial proportion of the stock of the slowest carbon pool.
- Carbon storage capacity of disturbed forest soils is potentially much higher than currently assumed.
- Century-term simulation of changes in soil carbon stocks that use spin-up-runs without the transient correction miss a considerable amount of carbon accumulation at many disturbed forest sites

Appendix A: Calculation of average litter inputs

In addition to the measured litter input, we calculated input by harvest residues and coarse roots after harvest in the following way. Merchantable timber volume and volume increment of the remaining part of the stand was estimated by yield tables (Dittmar et al. 1986). We assumed a harvest of 50% of the volume at age 140 years and 15%, 15% and 20% at the ages 150, 160, 170 years respectively. Carbon mass of tree compartments stem, branches were estimated by age and site index dependent conversion factors of (Wirth et al. 2004). Extracted wood volume on harvest was 92% of merchantable timber volume (Weber pers. comm). Carbon mass of harvest residues was calculated by the difference between stem/branch carbon and the carbon mass of the extracted wood by applying a wood density of 0.56 t/m^3 and a carbon concentration of 48.6% (Weiss et al. 2000). The harvest residues and roots were partitioned to the inputs of the Yasso model according to Table 4. The coarse woody part of harvest residues was removed by about 90% by wood pickers (Mund pers. Comm.). The sum of harvest residues and root biomass was divided by the rotation length of 140 years and added to the average litter inputs.

Appendix B: Parameterization of the Yasso model

Following tables list the standard parameters that have been applied to the Yasso Model for simulation experiments.

climatic parameters (standard climate)

mat0	3.3 °C	standard mean annual temperature
drought0	-32 mm	standard precipitation - potential evapotranspiration from may to september
beta	0.105	effect of mean annual temperature
gamma	0.00274	effect of drought

decomposition rates (k) and mass proportions of decay use to form more recalcitrant components (p)

compartment	k [1/yr]	p [1]	
ext	0.48	0.2	conifers
ext_b	0.82	0.2	deciduous
cel	0.30	0.2	
lig	0.22	0.2	
hum1	0.012	0.2	
hum2	0.0012	0	

standard relative sensitivity of slow pool decay rates to differences in temperature and drought

s1 (hum1)	0.60
s2 (hum2)	0.36

microbial invasion rates with standard climate

compartment	a [1/yr]
fwl	0.540
cwl_small	0.077
cwl_large	0.030

chemical composition of litter, used in the equilibrium experiment (Pinus sylvestris).

compartment	ext	cel	lig
nwl	0.27	0.51	0.22
fwl	0.03	0.66	0.31
cwl	0.01	0.69	0.30

chemical composition of litter, used in the Leinefelde application (broadleaved)

compartment	ext	cel	lig
nwl	0.38	0.36	0.26
fwl	0.03	0.65	0.32
cwl	0.01	0.77	0.22

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Effect of the Aggregation of Multi-Cohort Mixed Stands on Modeling Forest Ecosystem Carbon Stocks

Abstract Studies of the carbon sink of forest ecosystems often stratify the studied stands by the dominating species and thereby abstract from differences in the mixed-species, multi-cohort structure of many forests. This case study infers whether the aggregation of forestry data introduces a bias in the estimates of carbon stock changes at the scale of individual stands and the scale of a forest district. The empirical TreeGrOSS-C model was applied to 1616 plots of a forest district in Central Germany to simulate carbon dynamics in biomass, woody debris, and soil. In a first approach each stand was explicitly simulated with all cohorts. In three other approaches the forest inventory data were aggregated in several ways, including a stratification of the stands to 110 classes according to the dominating species, age class, and site conditions. A small but significant bias was confirmed. At stand scale the initial ecosystem carbon stocks by the aggregated approach differed from that of the detailed approach by 2.3%, but at the district scale only by 0.05%. The differences in age between interspersed and dominant cohorts as well as differences in litter production were important for the initial stocks. The amounts of wood extracted by thinning operations were important for the projection of the stocks over 100 years. Because of the smallness of bias this case study collects evidence that the approaches, that represent stands or stratums by a single cohort, are valid at the scale of a forest district or larger.

Keywords stand structure, thinning, scale, forest growth model, TreeGrOSS-C, inventory

Introduction

Forest ecosystems of the northern hemisphere are currently a large carbon sink in respect to the atmosphere (Liski et al. 2003, Myneni et al. 2001). The direct human-induced part of this sink is accountable with the Kyoto protocol (UNFCCC 1997). However, factoring out the drivers for this sink can only be done with large uncertainties yet (e.g. Albani et al. 2006, e.g. Vetter et al. 2005) and studies are required that better represent forest management, especially the effects of age and stand structure (Perry et al. 2008). In line with changes in forest management goals, many forests in Central Germany will become more diverse and the importance of mixed species, multi-cohort stands will increase (Gamborg and Larsen 2003, Kohm and Franklin 1997, Larsen and Nielsen). Many current studies of forest carbon, however, work with stratified forest inventory data (e.g. Vetter et al. 2005) and hence abstract from many details of the stand structure. This involves aggregation of inventory data, which potentially introduces a bias with the application of non-linear models (Harvey 2000). Several aspects of carbon stock quantification are highly non-linear, e.g. the dependence of biomass expansion factors on tree age and site quality. Hence, it needs to be tested, if the aggregation of forest inventory data and the representation of multi-cohort mixed stands results in a bias in carbon stock projections.

Davi et al. (2006) already showed that aggregating several eco-physiological parameters had only a negligible bias on applying the process based CASTANEA model at subplot, stand, and landscape scale. They simulated monospecific stands only. The factors that are generalized or averaged in the process of data aggregation at stand scale, however, concern mostly differences between species and between tree ages. First there are parameters of the growth and management of trees (diameter and height increment, competition, thinning intensities, natural mortality, proportion of extracted biomass on harvest), second, the conversion of inventory data to carbon mass (volume equations, wood densities, biomass expansion factors for stem, branches, leaves, and roots), third, estimation of carbon inputs to the soil (biomass turnover rates), and fourth, litter

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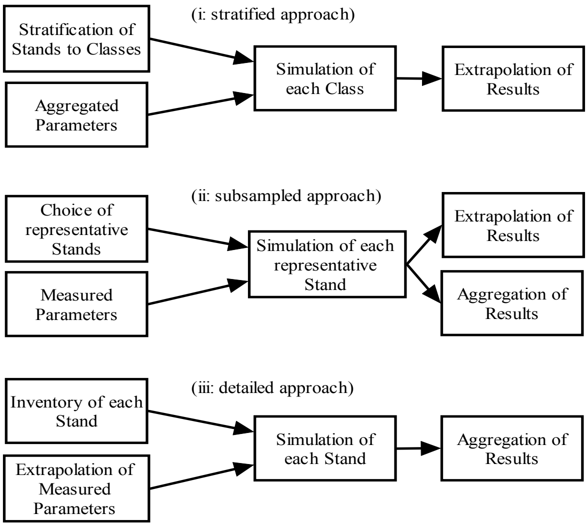


Figure 1: Classification of approaches of projecting carbon sink of a forest area. The approaches differ by first, the set of stands that are projected, second, by the spatial detail of inputs and parameters that drive the projections, and by the assumptions involved to extrapolate or aggregate the results of the projections.

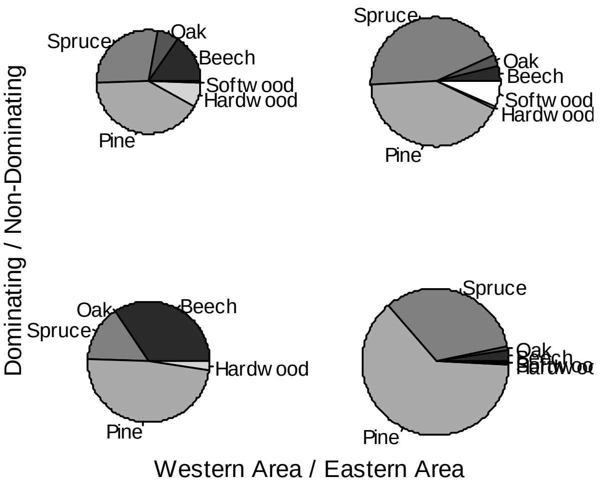


Figure 2: Distribution of Species Groups. There are less broadleaved species within the dominating cohorts compared to the interspersed cohorts in the Eastern growing region and more Beech dominated stands in the dominating cohorts of the Western region.

decomposition parameters (distribution of litter qualities and decomposition rates).

I categorize the approaches of projecting the forest carbon sink into three classes (Fig. 1). First, with the stratified approach (i) the forest area is stratified into classes by dominating species, age structure, and site conditions. Next, the carbon dynamics of each class are simulated (e.g. Freibauer et al. 2008, e.g. Vetter et al. 2005). Alternatively, the transitions of forest areas from one class to another class are tracked in a forest scenario model (e.g. Thurig and Schelhaas 2006). Second, the subsampled approach (ii) differs from the stratified approach by simulating a set of localized stands instead of a set of classes. The approach must assume that the sample of simulated stands is representative for the studied forest area (Lasch et al. 2005, e.g. Nabuurs and Schelhaas 2002). Third, the detailed approach (iii) simulates each stand of the study area separately (e.g. Le Maire et al. 2005). The level of spatial heterogeneity and the level of detail in forestry management that can be represented in the carbon sink projection increases from (i) to (iii). However, also the requirements on input data and execution times increase. Therefore it is desirable to use approach (i), but it must be shown, that the aggregation of parameters and input data does not lead to a bias.

Hence, the goal of this study was to perform a case study at the scale of a forest district that assesses the effect of the aggregation of the forest inventory data on the carbon stock projections. I used a single-tree based empirical forest ecosystem carbon balance model and compared the simulated carbon stocks between different scenarios of aggregating forest inventory data. My hypothesis was that the aggregation of multi-cohort forest inventory data to a single cohort results in a bias in simulated forest ecosystem carbons stocks. In order to exclude confounding effects, this study did not consider climate change and changes in management practises. The finding that the bias within this case study was small compared to the projected changes in forest carbons stocks collects evidence that the usage of stratified data in carbon stock projections is viable for quantifying carbon and projecting carbon stocks at scales of forest districts and larger.

Methods

Study area

I studied a population of forest stands in the Hummelshain forest district. The population was constrained to stands that were owned by the federal state, and where trees with a diameter at breast height (dbh) of at least 7 cm were present, because forestry inventory data were sparse or it were not available for other stands. The population consisted of 1616 stands that covered an area of 3619 ha. The Hummelshain forest district was located 50° 48′ N, 11° 35′ O at the south-eastern edge of Thuringian basin at altitudes of 270- 330 m above sea level. Limestone in the west and sandstone at the east of the district formed a plateau that was carved by the river Saale and several smaller rivers. The forest areas were located at the plateau areas and the ridges between the Saale and several contributing rivers. Mean annual temperature was 8.5 °C and annual precipitation was 602 mm according to the lower climate stratum of Vetter et al. (2005). Most stands were dominated by Scots Pine (*Pinus sylvestris*) and interspersed with Spruce (*Picea abies*), Birch (*Betula pendula*), and Oak (*Quercus rubra*). On several sites also Common Beech (*Fagus sylvatica*) was dominating. There were differences in species composition between the western sandstone dominated growing region and the eastern limestone dominated growing region (Fig. 2 bottom). The forest area has been managed until 1993 by a smallstrip clearcutting system leading to homogeneously managed stands of size 0.5-5 ha. For more than two third of the stand area the forest inventory recorded one or more cohorts in addition to the dominating cohort. Within the non-dominating cohorts there was a larger proportion of Oak and other Softwood and Hardwood species (Fig. 2 top).

I exemplify some of the stand-scale results at the specific stand named "10,S,1,3,189,a,2", which consisted of 4 cohorts (Table 1): the dominating Spruce cohort of age 55 years, a younger spruce cohort of age 45 years, a pine cohort and a birch cohort, which were both of age 50 years. The forest inventory additionally listed a remnant of a pine cohort of age 95 year, for which no further information, such as basal area, was available. Site conditions were described as a dystric Cambisol (class "BBn: Normbraunerde") on sandstone bedrock with no seasonal changes in intermediate soil moisture (class "terrestrisch, mäßig frisch") and intermediate nutrient availability. The stand is located in the climatic region in the lowlands (class "Vm"), with annual mean temperature of 8.5°C, annual precipitation sum of 602 mm, and a drought index, i.e. precipitation minus potential evapotranspiration from May to September, of 8 mm.

Data

Forest inventory in the study region is performed with the main objective to assess timber volume and growth increment. All the stands of the forest area of the forest district are sampled during one year and the sampling is repeated every 10 years. Diameter at breast height (cm) and basal area (m^2/ha) of each cohort (classified by species, age, and height distribution) are assessed with a relascope and on a small subset of trees tree height is measured. Cohort data enters a database together with recorded age of the cohort, measured or interpolated height (m), calculated relative and absolute timber volume (m^3/ha; m^3), site index (expected tree height at age 100 years in m), the proportion of covered area within a layer of the stand (%), a species identifier and several other descriptive parameters such as social role, tree layer and damages.

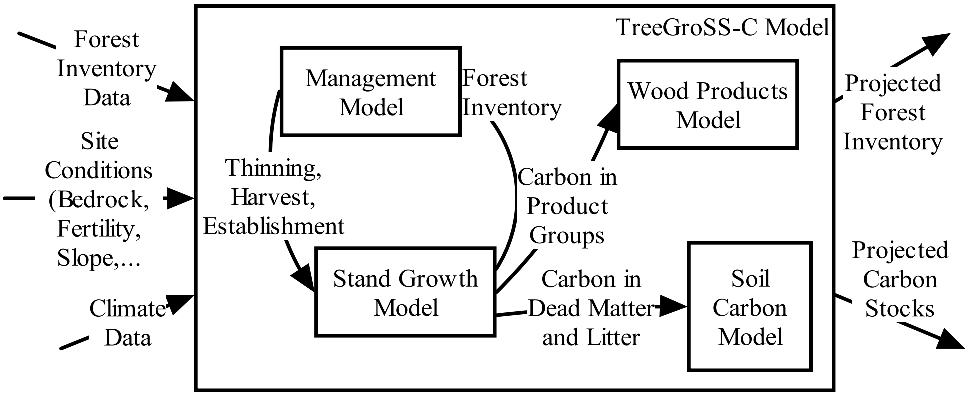
Additionally, an inventory of site conditions has been performed, which is based on soil profiles and delineation of homogenous areas based mainly on local topography and ground vegetation (Kopp and Schwaneke 1991). The site inventory records information on bedrock, geology, moisture conditions and nutrient availability. The areas of this site evaluation are nested within areas of similar climatic conditions, which are based mainly on altitude and exposition in this inventory.

I used the climatic data from (Vetter et al. 2005) and related it to the classes of the site inventory. Vetter et al. obtained the data from 11 stations of the German Meteorological Society (DWD Offenbach Germany) and aggregated it to 3 classes. The original data consisted of an hourly record of temperature, precipitation, water pressure deficit, solar radiation and day length from 1971-2001. Additionally I used the Simpel model (Hörmann 2006) to calculate potential evapotranspiration for spruce and for broadleaved species dominated stands.

Table 1: Inventory information for the stand „10,S,1,3,189,a,2“

species	age	diameter	height	coverage	basal area	volume
	yr	cm	m	% area	m^2/ha	m^3/ha
spruce	55	18	24	65	27	311
pine	50	26	22	15	27	271
birch	50	23	24	20	27	271
spruce	45	10	15	40	9	72
pine	95	41	?	?	?	6

Figure 3: Conceptual view of the TreeGrOSS-C model. Arrows denote inputs and outputs to the TreeGrOSS-C model and its submodels.



Forest Ecosystem Carbon Model

In order to project the stand structure and the development of carbon stocks, I used the TreeGrOSS-C model which is described in more detail in appendix A and (Wutzler 2007). The model is an extension of the TreeGrOSS-model (Tree Growth Open Source Simulator), an empirical single tree based stand simulator which is based on data of long term monitoring plots in Central Germany (Nagel 1999, Nagel 2006, Nagel 2003). TreeGrOSS projects the development of diameter and height of individual trees by a species and site dependent potential growth that is diminished by the competition state of each tree. It contains modules to calculate the timber volume of trees, as well as modules to generate distributions of single trees, based on average diameter and height of tree cohorts. I extended the TreeGrOSS model first, by modules to read and generate inventory information of the used inventory data, second, by modules to convert timber volume to carbon of several tree compartments and it's turnover by wood density (Weiss et al. 2000), biomass expansion factors (Lehtonen et al., Wutzler et al. 2008, Zianis et al. 2005), and average life times (Wutzler and Mund 2007), and third, by modules to allocate carbon in harvested timber to several product groups according to (Mund et al. 2005). Next, I coupled the extended TreeGrOSS model to a model of forestry management, a simple wood product model, and the Yasso Soil Carbon model (Liski et al. 2005) (Fig. 3). The management model compared the inventory of the simulated stand to yield tables at each year that was listed in the corresponding yield tables. Then it generated thinning demands by specifying the accumulated basal area and the mean diameter of trees to be thinned as the difference to the goal from the yield table. The amount of thinning was constrained to be at maximum 20% of the current basal area, in order to avoid stand instability. The stand was harvested at the last stand age that was recorded in the yield table of the dominating cohort and cohorts were re-established with the same shares of cohorts as in the initial forest inventory. The product model tracked the carbon in several product groups that are defined by a common life time. The Yasso soil carbon model was split into a species-dependent and a species-independent part. The dependent parts were replicated in order to simulate multi-cohort stands. Yearly inputs of mean annual temperature, annual precipitation, and drought index were provided. The soil model was initialized by spinup-runs with modelled mean past litter production (Wutzler and Mund 2007) and corrected with the transient correction to account for former disturbances (Wutzler and Reichstein 2007). The correction required an independent estimate of initial carbon stocks. Therefore, I extrapolated measured carbons stocks in mineral soil and organic layer based on the inventory of site conditions and the forest inventory. For the spatial extrapolation, I applied geo-matching in conjunction with the regression models developed by Wirth et. al. (2004), making use of the combined data of the forest inventory and the site evaluation. The stand growth model had an internal time step of 5 years. The management model and the product model were implemented as discrete event models (Zeigler et al. 2000) and run according to the thinning events as specified by the yield tables. The Yasso soil carbon model was implemented as a quantized system that solved the differential equations with a time step adjusted to the accuracy of the pool changes (Kofman 1997) and received updated litter input rates at least each 5 years.

In this study I analysed the simulated merchantable timber volume (m^3/ha), above ground wood with a diameter > 7cm and carbon stocks (t/ha) in

- above and below ground biomass of living trees
- woody debris, i.e. the sum of dead wood, dead root and woody litter
- and the soil including the organic layer

Practical Scenario

Because of the goal of this study was to assess the effect of the aggregation of multi-cohort multi-species stands to only one dominating cohort on the carbon stock projections, I did not introduce scenarios of climate change nor introduce changes in management practises. I project the carbon stocks to the next century under practical assumption that management, i.e. timing and amount of thinning and harvesting and stand establishment, corresponded to yield tables. Climatic drivers were kept constant to the mean over the previous 40 years. The additional assumptions with the possible inclusion of climatic correction into empirical stand growth models (Matala et al. 2006) together with the uncertainty of regional and topographic climate scenarios (Running et al. 1987), would have increased model complexity and they would also have complicated the interpretation of the results.

Four Approaches of Aggregating Forest Inventory Data

The aim of this study was to assess the effect of aggregating multi-cohort, multi-species stands to only one cohort on the projection of carbon stocks. Hence, I first ran the TreeGrOSS-C model with the data of all the stands and all the cohorts to form a baseline (detailed approach, Fig 1iii). Second, I ran the model for each stand but with only a single aggregated cohort, i.e. a monospecific stand (aggregated approach Table 2). The properties species, age, diameter, height, and site index of this aggregated cohort corresponded to the dominating cohort. The properties basal area, timber volume, and covered area of the aggregated cohort corresponded to the sum across all the cohorts within the stand. Third, I analyzed a subset of 46 randomly selected stands with all cohorts (subsampled approach). The number of 46 stands was chosen because there were 46 plots of the national forest inventory (BMVEL 2005) within the study area. And fourth, I aggregated all the inventory data into classes according to four species groups, age classes of 10 years, and three classes of site quality according to site index (Kramer and Akça 1995) (stratified approach, Fig. 1i). For each class I ran a simulation with one cohort using the data of site conditions and the climate record for the area that was most abundant within the forest area that was represented by the class.

Table 2: Approaches of aggregating the forest inventory data.

	Cohort aggregation	
Stand aggregation	**Detailed**	**Aggregated**
	Each stand	Each stand
	All cohorts	Single aggregated cohort
	Subsampled	**Stratified**
	Subset of 46 stands	110 strata of district inventory data
	All cohorts	Single aggregated cohort

Statistical Analysis

Mean carbon stocks at forest district scale and at the two sub regions of the Eastern and Western growing region were calculated with weighting the stands or classes by their corresponding stand area. In order to compare the significance of differences between the approaches I used a bootstrap analysis (Davison and Hinkley 1997) of 1000 times randomly sampling stands or classes with replacement. This mimics a 1000 times resampling of the forest district. From each bootstrap sample I recalculated the weighted mean of simulated carbon stocks (tC/ha) by one of the aggregated approaches and I recalculated its difference to the weighted mean of the stocks that were simulated by the detailed approach for each bootstrap sample. The mean, the standard deviation, and the 2.5% to 97.5% confidence interval of the difference were estimated from the empirical cumulative distribution function across the bootstrap samples. The bias, i.e. the mean difference to the detailed approach, was significant if the 95% confidence interval did not include the zero difference. In the same manner I calculated the differences between approaches and their statistics of the stock change (tC/ha/yr) from 2003 until 2013, 2023, 2053 and 2103. The bootstrap analysis is here more appropriate than t-tests or rank-tests because it accounts for booth, the strong non-normality of the distribution and the weights of each stand or observation.

Results

Stand Level

First, I compared the aggregated versus the detailed approach (Table 2) at single stands. The two approaches differ most by the consequences of different thinning operations and by different carbon mass per timber wood volume, i.e. the parameters wood density and biomass expansion factor. For example, at the stand named “10,S,1,3,189,a,2,0” less pre-commercial thinning or self-thinning was simulated with the aggregated approach (Fig. 4a). This was because of stronger thinning for the interspersed cohorts than for the dominating spruce cohort, which was prescribed by the yield tables. Further the species of the interspersed cohorts were also less shade-tolerant than the dominating cohort and the model calculated stronger self-thinning. This resulted in higher standing timber volume in tree biomass but in lower tree biomass because of differences in conversion factors. At the same time, less dead wood was produced with the aggregated approach. Hence, there were lower carbon stocks in woody debris and soil (Fig. 4b and 4d). Besides thinning, also differences in litter production and litter turnover between species were important for woody debris and soil carbon stocks. When ecosystem carbon stocks were compared, i.e. the sum of carbon stocks in above and below ground biomass, woody debris, and soil, the aggregated approach resulted in lower initial carbon stocks for the example stand (Fig. 4c). The differences in volume equations, wood density, biomass expansion factors and initial carbon stocks between species caused the difference in ecosystem carbon stocks at the beginning of the projection in 2003.

In addition, there were differences in initial woody debris carbon stocks (-7.3 to 2.9 t/ha in 95% of the stands) and soil carbon stocks (-19.0 to 11.9 t/ha) (Fig. 5). These differences were larger than the difference in biomass stocks (-1.2 to 8.8 t/ha) and dominated the differences in ecosystem carbon stocks (-21.8 to 16.2 t/ha). However, these differences in initial carbon stocks between approaches was small compared to the differences between the stands (Fig. 6). The relative difference

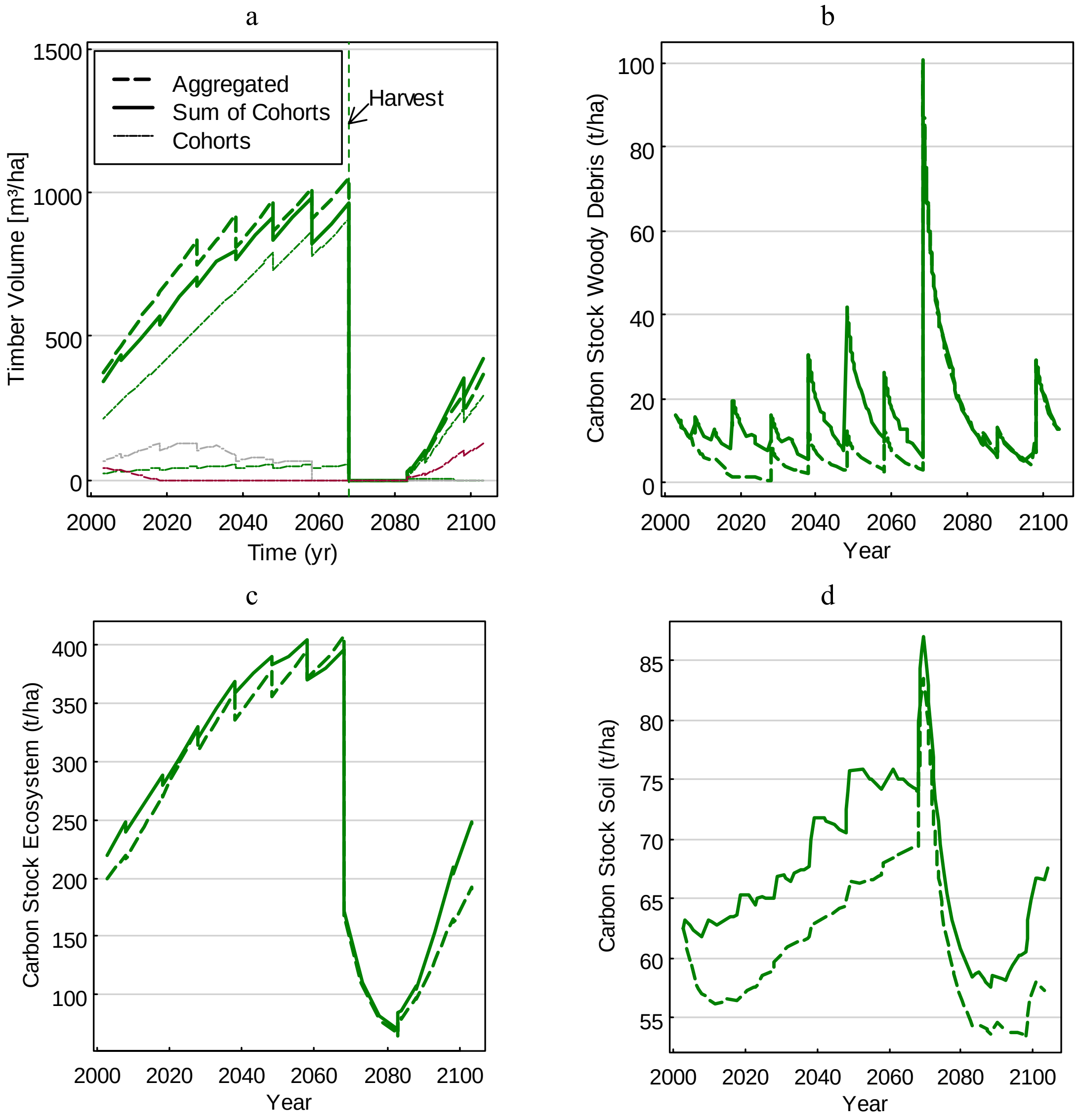


Figure 4: Stand scale differences of projections of timber volume (a), carbon stocks in woody debris (b), ecosystem (c), and mineral soil (c) between the detailed approach (soilid line) and the aggregated approach (dashed line). The several dash-dot lines in figure four correspond to the four simulated tree cohorts (Table 1) in the stand growth model.

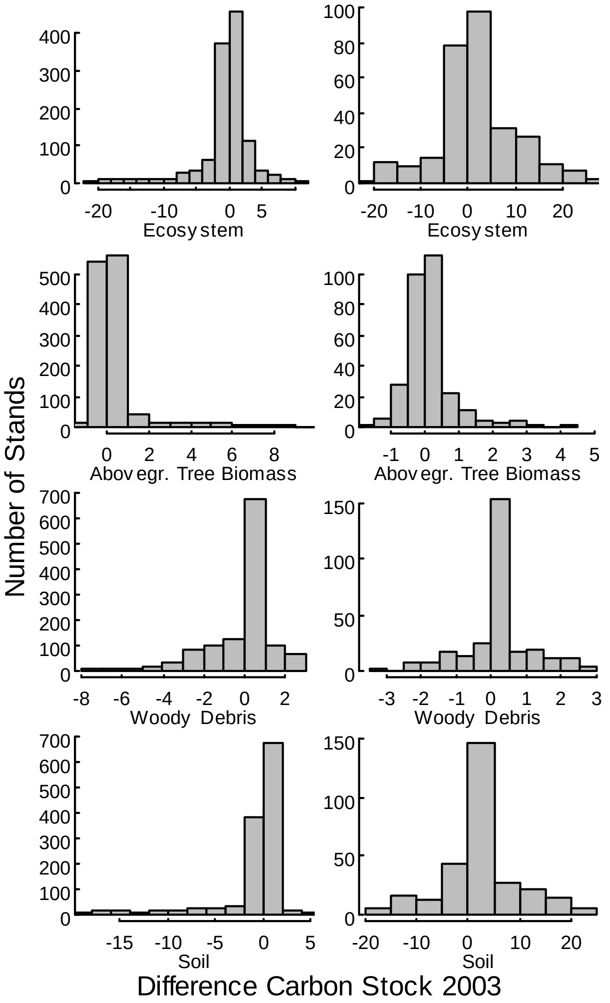


Figure 5: Histogram of the differences in 2003 carbon stocks between aggregated and detailed approach (C_{aggr}-C_{detl}). The left column represents the Eastern growing region and the right column the Western growing region. Note the different scale of the x-axis which represents the empirical 95% confidence interval.

Figure 6: Stand scale initial, i.e, year 2003, ecosystem carbon stocks (t/ha).

between the detailed and the aggregated approach of 2003 ecosystem carbon stocks did not exceed 2% for 71% of the stands. The mean of the absolute values of the differences was 2.3% and the standard deviation of the differences was 9.0%. However, eight stands differed by more than 20%. For a subset of the stands the carbon stocks were overestimated by the aggregated approach, but for the other stands the stocks were underestimated. The histograms (Fig. 5) showed no apparent dominance of a direction of the difference between the aggregated approach and the detail approach.

Forest District Scale

At forest district scale the bootstrap analysis detected a non-significant difference (-0.39 t/ha) in 2003 ecosystem carbon stocks between the aggregated and the detailed approach (Table 3). However, for the subsets of stands in the Eastern and the Western growing region there was a significant underestimation (-0.93 t/ha) and overestimation (+1.9 t/ha) respectively. The difference in the soil carbon stocks (95% of the bootstrap samples within -1.15 to -0.48 t/ha) was larger than the difference in biomass stocks (-0.78 to +0.015 t/ha) and in woody debris carbon stocks (-0.54 to -0.29 t/ha) (Fig. 7).

Further, when I compared the change in ecosystem carbon stocks between 2003 and 2023, there was a significant underestimation of these stock change by the aggregated approach of about -33 kg/ha/yr across the district and the sub regions. The difference regarding ecosystem stock change was dominated by biomass (95% of the bootstrap samples within -48 to -28 kg/ha/yr) compared to woody debris (+12 to +27 kg/ha/yr) and soil (-20 to -7 kg/ha/yr).

At district level, I could also compare the results of the subsampled and the stratified approach (Table 2) to the detailed approach. The studied population was the same, but the sample of individuals differed across the approaches. The box-plots of the distribution of carbon stocks in 2003 across the forest area showed that about 50% of the area had carbon stocks of 190 to 250 tC/ha and a median of about 220 tC/ha in all approaches (Fig. 8). The subsampled and the stratified approach did not represent areas of extreme (28 to 289 t/ha) carbon stocks. The bootstrap analysis showed comparatively wide confidence intervals (-24 to +14 tC/ha) for the difference in ecosystem carbon stocks 2003 between the subsampled and the detailed approach (Table 3). Hence, there was no significant bias detected. The bias with the stratified approach, i.e. the difference to the detailed approach, of 2003 ecosystem carbon stocks had the same directions for the regions as

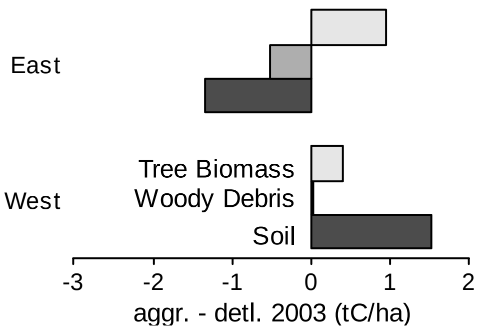


Figure 7: Differences in district mean carbon stocks 2003 between aggregated and detailed approach.

Table 3: Bootstrap statistics about the differences of the aggregating approaches from the detailed approach in 2003 ecosystem carbon stocks (t/ha). $q_{2.5}$ and $q_{97.5}$:empirical 2.5% and 97.5% percentiles, p_0 zero difference in the empirical cumulative distribution function (outside 0.025 and 0.975 is significant).

Region	Mean	Std.Dev	$q_{2.5}$	$q_{97.5}$	p_0	bias
Aggregated - Detailed						
District	-0.39	0.21	-0.78	0.015	0.97	trend of underestimation
East	-0.93	0.19	-1.3	-0.54	1.0	significant underestimtion
West	1.9	0.62	0.65	3.1	0.0020	significant overestimation
Subsampled - Detailed						
District	-1.9	10	-24	14	0.50	no
East	0.37	11	-22	17	0.46	no
West	1.0	5.8	-11	8.0	0.50	no
Stratified - Detailed						
District	-3.9	0.92	-5.7	-2.1	1.0	significant underestimtion
East	-6.1	0.98	-8.1	-4.2	1.0	significant underestimtion
West	5.4	1.8	1.9	9.2	0.0010	significant overestimation

Table 4: Bootstrap statistics differences in ecosystem carbon stock changes from 2003 to 2023 (t/ha/yr). Symbols as in Table 3.

Region	Mean	Std.Dev	$q_{2.5}$	$q_{97.5}$	p_0	bias
Aggregated - Detailed						
District	-0.033	0.0060	-0.043	-0.021	1.0	significant underestimation
East	-0.033	0.0071	-0.047	-0.019	1.0	significant underestimation
West	-0.034	0.011	-0.056	-0.011	1.0	significant underestimation
Subsampled - Detailed						
District	-0.012	0.27	-0.53	0.48	0.56	no
East	0.013	0.35	-0.51	0.61	0.46	no
West	0.017	0.15	-0.25	0.28	0.38	no
Stratified - Detailed						
District	0.48	0.031	0.42	0.54	0.0	significant overestimation
East	0.50	0.031	0.44	0.56	0.0	significant overestimation
West	0.41	0.091	0.23	0.58	0.0	significant overestimation

Figure 8:
Distribution of the 2003 carbon stocks (t/ha) across the forest area.

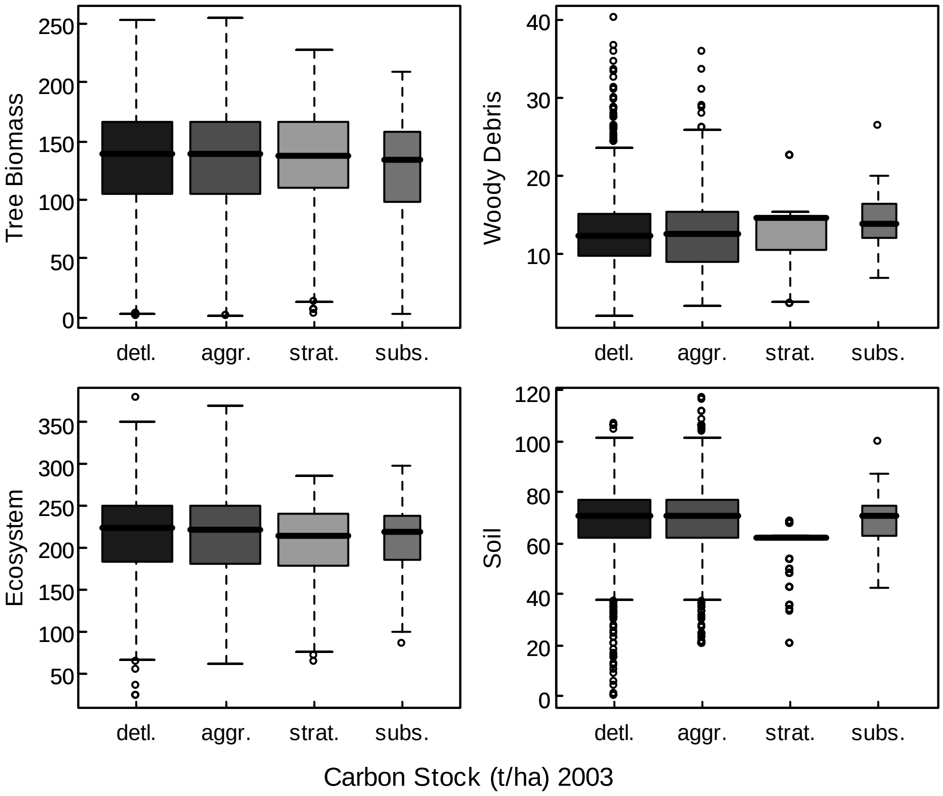
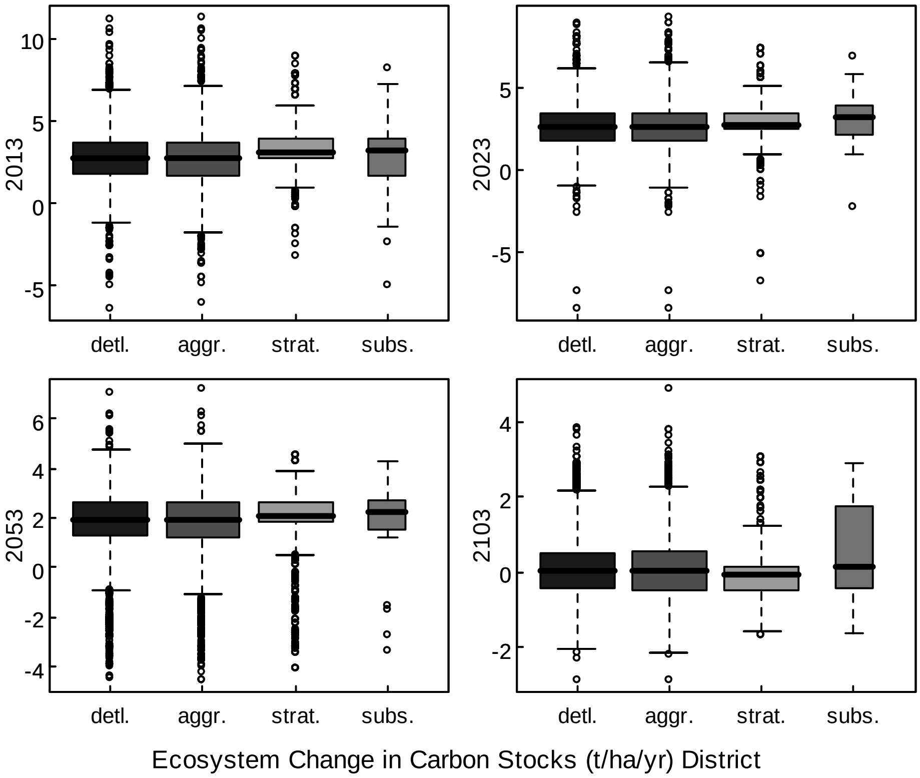


Figure 9:
Distribution of the carbon stocks change 2003-2023 (t/ha/yr) across the forest area for the detailed, aggregated, stratified, and subsampled approach.



with the aggregated approach, and the bias was significant for all regions.

When comparing the distribution of the carbon stock change between 2003 and the years 2013, 2023, 2053 and 2103, there were no obvious differences in the median and the quantiles of the distribution between approaches (Fig. 9). The subsampled and the stratified approach did not represent areas of the extreme carbon stocks changes. The bootstrap analysis of the carbons stock change from 2003 to 2023 found again large standard errors for the difference between the stratified and the detailed approach. Hence, this difference was not significant (Table 4). The stratified approach predicted a significantly larger stock change (0.48 t/ha/yr) than the detailed approach.

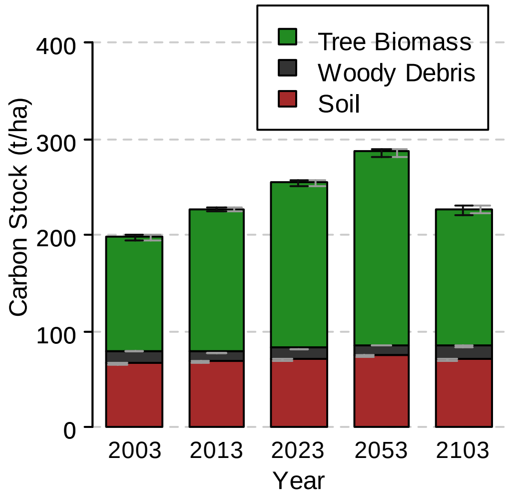


Figure 10: Forest district scale projections of carbons stocks. Black arrows represent the 95% bootstrap confidence interval of the detailed approach and grey arrows the intervals of the aggregated approach.

Discussion

This case study provides the first assessment of a potential bias in the quantification and projection of forest ecosystem carbon stocks with the aggregating forest inventory data of multi-cohort mixed stands. By driving a single-tree based empirical forest carbon balance model first with data on all cohorts and second with aggregated data (Table 2) it was possible to study the effect of abstracting from details of stand structure on the quantification of carbon stocks at the scale of stands and the scale of a forest district.

Our hypothesis which states that the aggregation of multi-cohort forest inventory data to a single cohort results in a bias in simulated forest ecosystem carbon stocks was first confirmed at stand scale. The difference in initial timber volume between the aggregated and the detailed approach is caused by differences in timber volume equations (Gregoire and Schabenberger 1996). With the example stand the aggregated approach, which subsumed the younger birch and spruce cohorts and the 10 years younger spruce cohort into the dominating spruce-cohort, resulted in a higher timber volume for the same basal area (Fig. 4). At the same time the approach resulted in lower carbon stock in tree biomass. This corresponds to the decrease of the biomass expansion factors with age (Lehtonen et al. 2007, Lehtonen et al. 2004, Wirth et al. 2004).

In addition, there were differences in initial woody debris and soil carbon stocks that were larger than the differences in biomass and differed between regions (Fig. 7). The difference in initial soil carbons stocks were caused mainly by differences in initial organic layer carbon stocks between coniferous and broadleaved species (Wirth et al. 2004) and to some extent also by differences in mean litter production (Wutzler and Mund 2007), and litter turnover (Liski et al. 2005).

The difference between the approaches in the predicted stock changes were mainly attributed to differences in thinning intensity in pre-commercial thinning and to differences in self-thinning between species in the example stand. The differences in diameter and height increment between species were less important (Fig. 4). This observation corresponds to the finding of the overruling effect of the thinning intensity of a similar forest in Central Germany (Wutzler et al. 2006). It also implies that a different representation of forestry management can significantly change the projection of the carbon sink during one rotation cycle.

At forest district scale the positive and negative deviations between the aggregated and the detailed approach balanced each other to a large extent (Fig. 5). Nevertheless, the size of the studied population was large enough so that the bootstrap analysis detected a trend of an overestimation at the district scale and an under and overestimation at the Eastern and Western growing region respectively (Table 3). However, this bias due to aggregation of stand data was small compared to the stocks and their changes (Fig. 10). The compensation of the bias at district scale might have been due to the fact that most of the interspersed species also occurred as dominant species. Therefore, I repeated the analysis independently for the Eastern and the Western part that differed in many aspects, most important in bedrock and species distribution. Although, there was a difference in the share of broadleaved species in the interspersed cohorts compared to the dominant cohorts within these regions (Fig 2), still negative and positive bias compensated so that the bias at district scale was small (Table 3). The disappearance of effects that are important at stand scale was also observed and discussed for environmental parameters in a monospecific process based forest growth model (Davi et al. 2006). From a theoretical perspective this is only expected, if the participating processes are linear (Harvey 2000). However, this was not strictly the case with our study as it was with Davi's study.

The opposing sign of the bias in the Eastern and the Western region allows us to discuss which reasons hindered a full balancing at the district scale. A possible reason for the bias ecosystem carbon stocks in 2003 is that spruce cohorts of age 50 years store about one third less carbon for the same timber volume compared to beech cohorts due to differences in wood density and biomass expansion factors (Löwe et al. 2000, Wirth et al. 2004). The interspersed cohorts have a larger contribution of broadleaved species compared to the dominating cohorts in the Eastern region and a smaller contribution in Western region respectively (Fig. 2). The aggregated approach subsumes a part of these cohorts within the dominating cohort. I, henceforth, expect an underestimation of biomass carbon stocks in the Eastern region and an overestimation in the Western region. Instead I observed a significant overestimation of biomass carbon stocks (+0.94 and +0.40 tC/ha) in both the Eastern and the Western region respectively with the larger overestimation in the Eastern growing region (Fig. 7). This is opposite of the expected differences and I, hence, think that this first reason has only a minor effect. A second possible reason is that interspersed cohorts are of different age than the dominating cohorts. At the Eastern region the dominant cohorts were on average (basal area weighted mean) one year younger than the interspersed cohorts and at the western region 11 years older. Hence, I would expect an overestimation of carbon stocks by the aggregated approach in the Western region. This is in line with the observed carbon stocks (Fig. 7). This second reason is likely a major contributor to bias in carbon stocks. A third possible reason is that the most broadleaved species have a higher mean litter carbon production than spruce and pine across the rotation cycle (Wutzler and Mund 2007). Therefore, I expect an underestimation of carbon stocks in woody debris and initial soil carbon in the Eastern region where broadleaved species are subsumed to pine and spruce cohorts. This is in line with a significant underestimation (-0.52 and -1.35 t/ha) in the Eastern region and an overestimation (0.02 and 1.52 t/ha) in the Western region for woody debris and soil carbon respectively. Because of the fact that differences in the approaches were mostly attributed to woody debris and soil (Fig. 7), this mechanism has a likely major effect on bias on carbon stock quantification.

The significance of the bias does not necessarily imply that this bias is important. When I compare the bias with the magnitude of the stocks and their changes (Fig. 10), the bias can hardly be presented in the graph and also the bias of the subsampled and stratified approach would hardly be seen. It is small compared to the range of the uncertainty of the ecosystem carbon stock prediction of the detailed approach (e.g. -0.39 tC/ha bias; 195.5 to 201.2 tC/ha 95% confidence interval of the detailed of ecosystem carbon stocks in 2003, i.e. only about 7% of the uncertainty range). The bias is small enough compared to the uncertainty range, so that I conclude that it is not important for the quantification and projection of carbon stocks at our case study. This study considered only uncertainty introduced by sampling the population of forest stands and the aggregation of the inventory data. If the uncertainty of the forest inventory and the model were considered, the uncertainty ranges would increase, and the relation of the bias to the uncertainty range would be even smaller. In order to verify that the smallness of the bias is a general phenomenon, it is necessary to repeat similar studies at various forests. However, I do not expect the bias to increase at other forests to the magnitude of the uncertainty range.

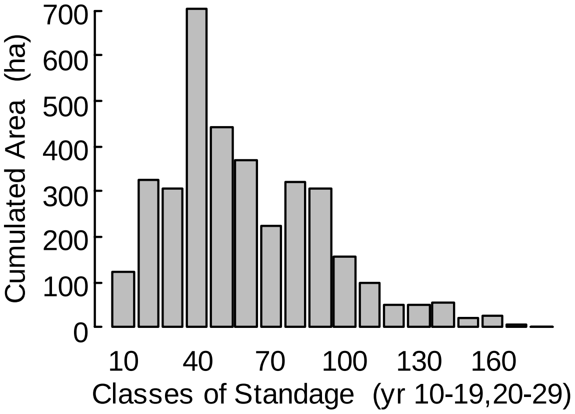


Figure 11: Age-class structure of the forest district.

The observation of higher simulated carbon stocks in woody debris and soil for spruce stands that are interspersed with broadleaved species counteracts with the observation of lower timber volume (Fig. 4a). Such antagonistic effects of mixture on productivity are observed, when species compete for the same resources (Pretzsch, 2003). However, our results confirm that a lower timber production of mixed stands does not imply lower carbon storage, which corresponds to findings by Jandl et al. (2007a).

All four studied approaches agreed in the temporal development of carbon stocks. All four approaches projected a shift in the distribution of carbon with time (Fig. 10). This shift is explained by the unbalanced age class structure in the forest district (Fig. 11). Initially there was a dominance of stands of age class 40-50 years and this dominance persisted in time, as the respective stands grew older. Ecosystem carbon stocks were dominated by the tree biomass stocks, which are larger at higher age classes. When it comes to harvest of these cohorts after 2053, the carbon stocks decrease again until 2103 (Fig. 10). This legacy effect of age classes has already been simulated before for the study region (Böttcher 2007, Vetter et al. 2005). Since, this age class effect is also observed in other regions of the world (Albani et al. 2006), it contributes to the projected exhaust of the terrestrial sink (Canadell et al. 2007).

The advantages of using an empirical distance independent tree based forest ecosystem carbon balance model are that I were able to run it at each individual stand including the full inventory data of all cohorts. I could take detailed account for site quality, as expressed by the site index, and for the effects of thinning operations on stand development. The drawback of this approach, however, was that I could not explicitly represented climate change in the stand growth submodel. Contrary, mechanistic approaches allow more confidence in longer term projections that are effected by changing environmental conditions, but require more detailed input parameters and input data (Grote and Pretzsch 2002, Matala et al. 2003, Porté and Bartelink 2002). With explicitly accounting for climate change I expect the stand growth and the biomass carbon stocks later than 2003 to be higher than with the presented simulations (Jandl et al. 2007b, Mund et al. 2002). The soil carbon either may be higher because of enhanced litter input or be lower because of enhanced decomposition of soil organic matter. Climate change could, however, effect species differently and alter competition, growth, and self-thinning. On the other hand, the changes in biomass carbon stocks are mainly a result of a changing age structure and thinning intensities in these managed forests. Therefore, I expect the effects of climate change in the next 100 years to be overruled by forestry management to a large extent.

Despite these disadvantages, our case study provides evidence, that the bias in carbon stock changes due to aggregation of stand data is only 7% of the uncertainty range, i.e. 95% confidence interval of the detailed approach, and hence our study provides evidence that the application of the aggregated and the stratified approaches are valid.

Conclusions

This case study on the potential bias, which is introduced by representing multi-cohort mixed forest stands by only one tree cohort, confirms a small but significant bias. It is based on several scenarios of aggregating forest inventory data of 1616 stands of a forestry district in Central Germany a single-tree based empirical forest carbon balance model. At stand scale the ecosystem stocks that were quantified for 2003 with the aggregated approach differed from the detailed approach by 2.3%, but at the district scale only by 0.05%.

The sign or the magnitude of the bias in simulated biomass, dead organic matter, and soil carbon stocks differed between two sub regions. By comparing the differences between the regions to the bias in carbon stocks I identified possible major causes for the bias. For the quantification of the initial stocks the differences in age between interspersed and dominant cohorts were important as well as differences in litter production between species. For the projection of the carbon stocks over the next 100 years, the differences in forestry management were important, namely the amounts of wood extracted by thinning operations.

Because of the smallness of bias, e.g. only 7% of the size of the 95% confidence interval of the detailed approach for the carbon stocks in 2003, this case study collects evidence that the approaches of carbon stock quantification, that represents stands or stratums by a single cohort, are valid at the scale of a forest district or larger.

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Appendix A: The TreeGrOSS stand growth model

The TreeGrOSS (Tree Growth Open Source Software) model (Nagel 2003) is a public domain variant of the BWinPro model (Nagel et al. 2002). According to the classification of Porté and Bartelink (2002) it belongs to the class of non-gap distance-independent tree models. The empirical model is based on a growth and yield experiment data pool of about 3500 plots in northern Germany. It uses the potential growth concept (Hasenauer 2006), which reduces species and site dependent potential relative height growth of a top height tree $i_{hrelPot}$ by the single trees competition situation (A1).

$$i_{hrel} = i_{hrelPot} + p_1 (h_{100} / h)^{p_2} \qquad \text{(A1)}$$

Where p_i are species specific constants, h_{100} is the topheight of the stand, i.e. the average height of the highest 100 trees, and h the height of the considered specific tree. The basal area growth of a tree is estimated by Eq. A2.

$$\begin{aligned} \ln(\Delta a_{Basal}) = {} & p_0 + p_1 \ln(c_S) + p_2 \ln(age) \\ & + p_3 c_{66} + p_4 c_{66c} + p_5 \ln(\Delta t) \end{aligned} \qquad \text{(A2)}$$

Where p_i are species specific constants, c_S is the crown surface area calculated from diameter, height of the tree, and the topheight of the stand, age is the tree age, Δt is the time period of usually 5 years, c_{66} is the competition index (Fig A1) and c_{66c} is an index that increases when the competition situation is relieved, i.e. neighbouring trees are thinned.

Further, I extended the model by thinning routines based only on information of the sum of basal area and mean quadratic diameter of thinned trees. These routines selected trees randomly from a probability distribution of tree diameters (Fig. A2). Eventually, I used one side of a Gaussian distribution with a mean of the cohorts minimum or maximum diameter, respectively to thinning from below or above, and a standard deviation chosen in a way, so that the expected quadratic mean diameter of thinned trees was equal to the specified one. The model and the extensions were validated against plot data of several permanent sampling inventories of both monospecific and multi-cohort multi-species stands within the study region. An example is shown in Fig. A3. The TreeGrOSS model performed at least as good as local yield tables with significant improvements for co-dominant and suppressed cohorts.

The complete time series, which at several stands covered more than 100 years, were kindly provided by the Eberswalde forestry research institute and the chair of Forest Growth and Timber Mensuration at TU-Dresden and preprocessed by Mund et al. (2005).

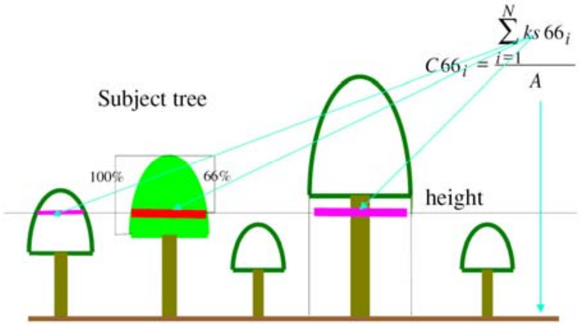

Figure A1: Calculation of the competition index in TreeGrOSS (taken from Nagel 2003). At a height of 2/3 (or 66%) of the crown length all crowns are cut, if they reach that height. If the crown base is above the height then cross sectional area of that tree will be taken. The sum of the cross sectional area is divided by the stand area.

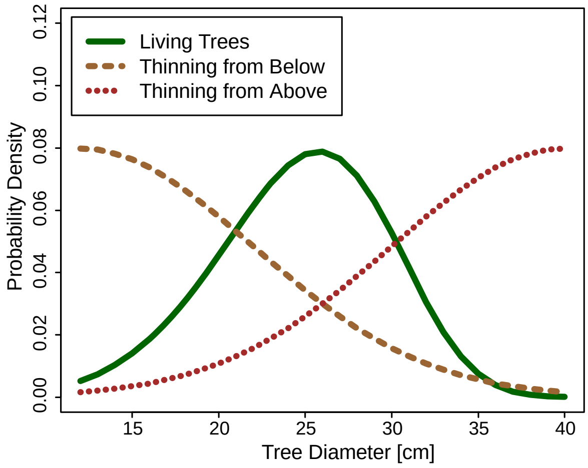

Figure A2: Selecting trees for thinning in the model by a probability distribution of tree diameter.

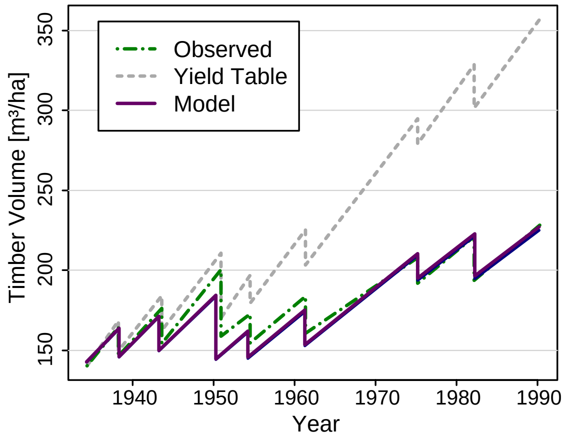

Figure A3: Comparison of inventoried timber volume from a suppressed beech cohort of the permanent inventory plot Leinefelde 245 to model predictions by a yield table (Dittmar et al. 1986) and predictions of the TreeGrOSS model.

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Selbstständigkeitserklärung

Ich erkläre, dass ich die vorliegende Arbeit selbstständig und unter Verwendung der angebenen Hilfsmittel, persönlichen Mitteilungen und Quellen angefertigt habe.

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