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Carbon Stocks in Danish Forest Types

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Abstract

As part of international agreements, countries are now obliged to monitor their greenhouse gas emissions as well as to report their possible sources and sinks. Carbon dioxide is one of the six greenhouse gases listed in the Kyoto Protocol, contributing to global warming. Research is conducted to gain knowledge on how to maximise forest carbon storage capacity, albeit, there are some constraints and limitations to both the role of forests in CO_2 mitigation efforts and the estimation and comparison of forest carbon stocks. Forests provide multiple services which might be in conflict to a management strategy solely addressing carbon storage. The estimation and comparison of forest carbon stocks is insofar limited as for instance studies use different definitions for dead wood and different soil depth. With respect to a changing climate, forests are subjected to changes that are not fully predictable yet.

In this study, I have examined the effect of stand age, soil category, tree species, crown cover, broadleaf fraction, tree species biodiversity, precipitation as well as previous land use on biomass, dead wood, forest floor and soil carbon stock on Danish forests. The main influence derives from stand age, soil category, tree species and crown cover. Depending on the carbon pool one to two of these variables explain more than 50% of the variation in the respective model. In general, older forests contain more C than younger ones. With increasing age, the biomass volume grows and the forest floor develops, thus, accumulates C. Each soil category is characterized by its properties, which among others determine the turnover rate of SOM, and consequently influencing the soil C stock. The tree species significantly influence the C stocks due to their different litter quality and root system. On average, a high crown cover indicates bigger biomass volumes and hence, greater C stock. Previous land use significantly influences only the forest floor C stock. The relative C stocks are similar to the absolute ones; here the soil C pool differs most, were e.g. the effect of broadleaf fraction and biodiversity enters the model. Furthermore, other factors such as forest management and the market for forest products influence C storage. The former especially affects the dead wood, forest floor and soil C stock. The wood market in turn, influences the forest management and gives an explanation for the average age of tree species. In total, broadleaf forests and forests on organic soil category contain the most C. The average soil C stock amounts to 184 tC ha^{-1}, the biomass C stock contains 81.2 tC ha^{-1} on average, about 1.16 tC ha^{-1} is stored in dead wood and 15.3 tC ha^{-1} in forest floor.

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List of Abbreviations

AFF	Afforested forest
BVOC	Biogenic Volatile Organic Compounds
°C	Degree Celsius
C	Carbon
CO_2	Carbon dioxide
DBH	Diameter at Breast Height
FLEGT	Forest Law Enforcement, Governance and Trade
FRF	Forest remaining as forest
GHG	Greenhouse Gas
GIS	Geographical Information System
GLM	General Linear Model
GPP	(annual) Gross primary production
Gt	Gigatons
ha	Hectare
LIDAR	Light Detection and Ranging
LSmean	Least Square Mean
LULUCF	Land Use, Land Use Change and Forestry
N	Nitrogen
NFI	National Forest Inventory
Pg	Picogramm
PLU	Previous Land Use
ppm	Parts Per Million
PSU	Primary Sampling Units
r^2	Coefficient of determination
REDD	Reducing Emissions from Deforestation and Forest Degradation
SOC	Soil Organic Carbon
SOM	Soil Organic Matter
SSU	Secondary Sampling Units
Std. Err.	Standard Error of the Mean
t	Metric tons
Temp. unst.	Temporarily unstocked
TSU	Tertiary Sampling Units
UNFCCC	United Nations Framework Convention on Climate Change
VOC	Volatile Organic Compound
yr	Year

1. Introduction

1.1. Background

In the 1960/70s, it was first noticed that the atmospheric CO_2 concentration was increasing and that it could be correlated to an increase of global temperatures (UNFCCC n.d. (c)). More than two decades later, it found widespread agreement among scientists that this development should be counteracted. Therefore, international agreements to reduce greenhouse gas emissions have been reached (UNFCCC n.d. (a)). These agreements encompass greenhouse gas inventories, implying, among others, accurate measurements as well as transparent reporting of CO_2 emissions and C stock changes. Moreover, the gained information on national C stocks and development need to be comparable among each other. Taking CO_2 emissions as an example, it was and still is necessary to gain a better understanding of the processes affecting carbon sequestration and storage, in order to be able to manage forests appropriately and set the right policies. According to UNEP et al. (2008) "a sink is any process, activity or mechanism that removes a greenhouse gas, an aerosol or a precursor of a greenhouse gas or aerosol from the atmosphere. […] The uptake of CO_2 in a reservoir, whether natural or artificial is also called carbon sequestration."

Trees, grasses as well as most other plants are able to take up CO_2 via photosynthesis. Carbon is stored in biomass, dead wood, forest floor (O-Horizon) and soil when the net primary production in an ecosystem is higher than the heterotrophic respiration rate (Vejre et al. 2003). Comparing tropical, temperate and boreal forests (including vegetation and soil to 1 m depth), most carbon, 408 t C ha^{-1}, is stored in boreal forests, followed by tropical forests with 243 t C ha^{-1}. Temperate forests store far less carbon, averaging only 152 t C ha^{-1} (18.9%) (IPCC 2000), comprising the smallest total area (5% of the world's forest area (Lorenz & Lal 2010)) of the three major forest biomes. Forests as a whole display a huge sink for C but can also become a source for C emissions due to human induced deforestation, especially in the tropics (Pan et al. 2011). Therefore, terrestrial ecosystems play a major part in the global C cycle.

1.2. International agreement on reporting forest carbon

At the United Nations Conference in Rio de Janeiro in 1992, countries admitted the increasing global temperature and confessed the importance of limiting greenhouse gas (GHG) emissions by launching the United Nations Framework Convention on Climate Change (UNFCCC). Along with the Kyoto Protocol signed in 1997 and entered into force in 2005, signatory countries were now obliged to conduct annual GHG inventories, including the Land Use and Land Use Change and Forestry (LULUCF) sector, to report their emissions by sources and sinks as well as their achievements in limiting GHG emissions. For the latter, countries get carbon credits with which they can trade (art. 6 Kyoto Protocol). As stated in art. 3.1 of the Kyoto Protocol, all Annex I countries are compelled to achieve an overall emission reduction of at least 5% compared to the level of the year 1990 (and 1995 for industrial gases) in the first commitment period 2008 – 2012 (United Nations 1998). The European Union committed itself to an 8% reduction (United Nations n.d.). The EU burden sharing agreement lead Denmark to set an emission reduction target of 21% (UNFCCC 2002b).

Guidelines for the GHG's inventories were established by the Intergovernmental Panel on Climate Change in 2002 (UNFCCC 2002a). The inventory for the UNFCCC within the LULUCF sector implies five carbon pools, namely above- and belowground biomass, dead wood, litter and soil organic C with uncertainty estimation at a confidence interval of 95% (IPCC 2003). These pools are also an integral part of fulfilling the Kyoto Protocol requirements (art. 3.3 and 3.4). To be able to report the GHG emissions for the forest sector, including a differentiation between the above mentioned four C pools, countries undertake a National Forest Inventory (NFI). Besides the estimation of the C stock size, the data can be used to determine the degree to which certain aspects, like stand age or tree species, influence the C stock in both the different pools and in total (all pools combined). However, soil C pools that turn out not to be a source of C emissions could be excluded from the inventory (United Nations 1998). Denmark applies the "non-source" principle, meaning that it will not report C fluxes in forest soils since it is proved that they are not a source for C emissions (Sverrild et al. 2009).

Reports on forest C, like national forest inventories, not only reveal the amount of C accumulated in forests in the respective inventory year, it has also made it possible to follow changes in the forest C budget over the years. A further aspect of C reporting is to set a baseline for trading with carbon credits. Moreover, instruments exist that address the reduction of deforestation. For example within the Clean Development Mechanism, developed nations have the possibility to offset their C emissions by financially supporting developing countries e.g. to conserve their forests or to support carbon mitigation projects (UNFCCC n.d. b). Another method for deforestation reduction, which is not part of the Kyoto Protocol, is the REDD(+) concept. It aims at reducing emissions from deforestation and forest degradation in the context of C trading (FAO et al. 2008). In addition, private certification schemes, such as the Forest Stewardship Council, or other voluntary partnership agreements like the Forest Law Enforcement, Governance and Trade action plan (FLEGT) of the European Union, contribute to the attempt by substituting clear cuts and illegal logging with substituting sustainable forest management and strengthening good forest governance of participating countries (European Forest Institute n.d.). However, these methods also have constraints. Basically, they will only function properly, if forested areas yield a higher price than the conversion to agricultural fields. In other words, they will only function if they can be implemented in an economically reasonable way (FAO 2012; Lorenz & Lal 2010).

1.3. Estimating forest carbon

As forests are heterogeneous ecosystems, it is difficult to estimate the C stock and fluxes over large areas. Common problems include the comparison or combination of results of independently conducted sampling designs of forest C pools within the same type of ecosystem. Sufficient data has to be collected to guarantee a statistically sound analysis (Jia & Akiyama 2005).

The best established method for measuring C in forests is based on statistically correct sampling designs, including permanent sampling plots and a division in forest C pools (Brown 2002; Jia & Akiyama 2005), as it is conducted in Denmark. Nevertheless, it is challenging to assess soil C stocks due to the inhomogeneous nature of soil ecosystems (Grace 2004). Most soil surveys are restricted to 100 cm depth. Jia & Akiyama (2005) criticise this fixed number and argue for enlarging the sampling depth, because there are great variations over the landscape which in turn impact the size of the soil C pool and thereby, the total forest C pool. For example in their study, an extension of the sampling depth to 300 cm led to an increase in soil C stock of 24% in comparison to 100 cm depth. In addition, soil C stock are exposed to overestimations if no correction of the bulk ratio of rocks is being made (Jia & Akiyama 2005).

Biomass and dead wood biomass are directly calculated from the tree measurement data by using biomass expansion factors or regression equations. However, those equations bear some uncertainties, too (Mäkipaä et al. 2008). Biomass equations are restricted mainly due to their poor representativeness on a national-scale. In most cases they are based on only a few felled sample trees on a few number of sites (Mäkipaä et al. 2008). A comparison with other studies is not always possible since different equations for calculating the biomass volume are applied.

For calculating dead wood biomass, a decomposition factor (depending on decomposition rates) is used with which the wood density is determined. This might cause wrong results because such a correlation does not always exist. Heartwood, for instance, is very resistant. It can still have a very high density even though it has already lost the bark and sapwood, which leads to a wrong classification of decomposition rate (Brown 2002). Comparison of dead wood contents in forests among countries and studies is rarely possible since most countries only have begun to conduct dead wood inventories. Additionally, different definitions of dead wood hinder a harmonization of national forest inventories yet, some countries only measure standing dead wood, while others also include coarse roots. What is more, the minimum diameters for both standing and lying dead wood vary with country (Woodall et al. 2009). In total, Jia & Akiyama (2005) indicate that the C storage of vegetation can be underestimated by about 12%, at least in cool-temperate forests, if standing dead trees and coarse woody debris are left out of the analysis (Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005)(Jia & Akiyama 2005).

Bradford et al. (2010) found that aboveground biomass has by far the highest sampling requirements compared to aboveground dead woody biomass, forest floor and soil (in increasing order), in order to ensure valid estimation of this C pool. Dead wood C pool requires more sampling plots than for both forest floor and mineral soil C pool. Regarding the size of the sampling plots, it is most efficient to sample a greater number of smaller individual plots, that are spread over the study area instead of large plots or plots grouped into clusters (Bradford et al. 2010).

In the future, measurements of forest biomass C might be conducted via remote sensing (Bradford et al. 2010; Grace 2004; Brown 2002). Especially the canopy height measuring LIDAR (light detection and ranging) sensor is a promising technique to monitor the world's forests. Combined with the Earth Systems Science Pathfinder programme, developed by NASA, it measures maximum canopy height, vertical distribution of canopy elements and surface topography below the vegetation canopy. On small scales, dual-camera digital videos are coupled with a pulse laser profiler, data recorders and differential GPS. Fixed on a single engine airplane, it collects images that are transformed to 3D models of the terrain, from which it is possible to gain the number of stems per unit area, the crown area, the tree crown density and the tree height (Brown 2002). These new techniques will help to provide a more complete image of the global forest C pool.

A predictive model not only for absolute but also for relative forest C stocks, including a differentiation between the forest C pools, is another way of estimating forest C. Using this model, it might not be necessary to conduct costly inventories every year.

2. Literature review

2.1. The global carbon cycle

The natural and human induced C cycle encompasses atmosphere, terrestrial biosphere and oceans (Fig.1). Out of these three pools, oceans are the biggest C reserves (>38,000 Gt). The terrestrial biosphere contains about 2,300 GtC (2/3 accounting to the soils (Malhi 2002)) and the atmosphere approximately 760 Gt (Fig. 1). Having a rather small pool, atmospheric C is relatively active in terms of its exchange rate with the other two reservoirs. The main flux is between the land and the atmosphere, in which the exchange between forest ecosystems and atmosphere is the most significant in the short-term C cycle (<100,000 years). In this cycle, atmospheric C is taken up via photosynthesis and returned to the atmosphere as CO_2 and CH_4 through respiration by plants, animals and microbes (Lorenz & Lal 2010).

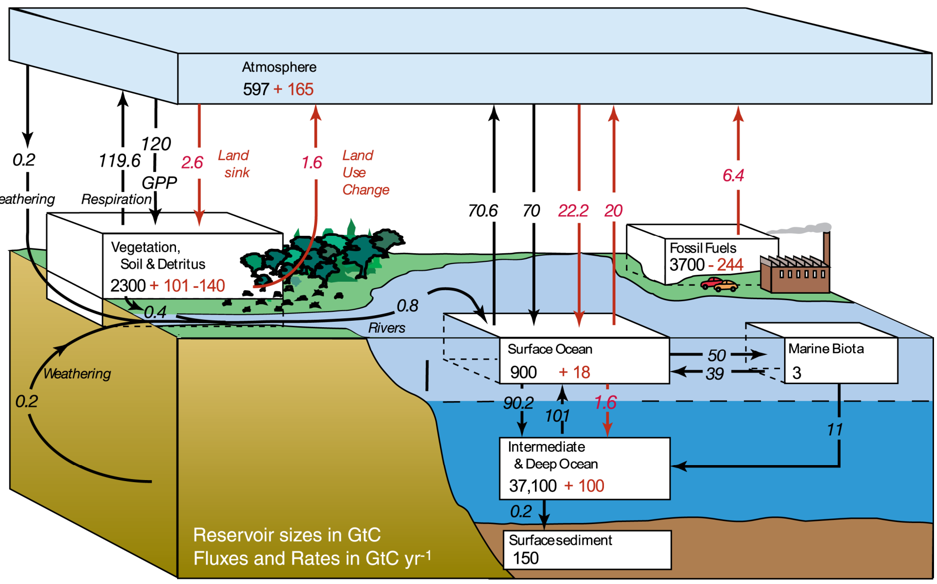


Fig. 1. The global carbon cycle with data for the 1990s, showing the main annual pre-industrial fluxes in GtC yr^{-1}. The red lines indicate anthropogenic fluxes, the black ones show natural fluxes. GPP is the terrestrial annual gross primary production (IPCC 2007b).

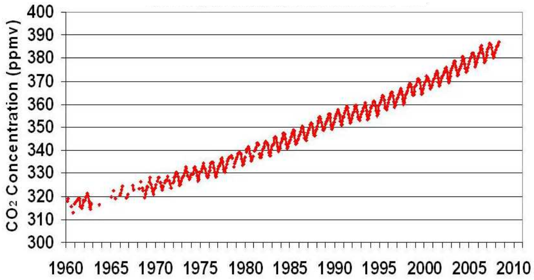
About 120 GtC yr^{-1} from the atmospheric C stock is transferred to the terrestrial biosphere via plant photosynthesis (depicting the Gross Primary Production, GPP). This is almost 16% of the total atmospheric C stock. At the same time, almost the same amount is returned to the atmosphere due to autotrophic and heterotrophic respiration. This process is dependent on temperature, precipitation, atmospheric CO_2 and nutrient availability. The transfer to the soil C pool varies with the type of soil and the microbial community (IPCC 2007b). Small fractions are exported from this flux by herbivores or other animals (Malhi 2002). About 90 GtC yr^{-1} are flowing between the oceans and the atmosphere, while only 0.6 GtC yr^{-1} is exchanged from land to the oceans. Atmospheric C is transferred to the oceans in form of CO_2 by physical dissolution forming HCO_3 and $CO^2{}_3$. The main uptake and release of C due to photosynthetic processes and decay or death occurs at the surface (euphotic zone). Most of it remains in the depth of the ocean, and a small fraction is embedded in the oceans' sediments (IPCC 2007b).

An atom of C has a residence time of about 300 years in the ocean (Meier-Reimer & Hasselmann 1987). However, most of the oceanic C is recycled in the surface zone within a couple of days (Eppley et al. 1983) to a year (Malhi 2002), depending on regional conditions affecting the export and transport of C within the ocean layers (Lutz et al. 2002; IPCC 2007b). The residence time of C in terrestrial biosphere and atmosphere is higher than in the surface layer of the ocean but far lower of that in deep ocean: about 17 years in the terrestrial biosphere, including 12 years in the soil, and about 4 years in the atmosphere (Malhi 2002). As C is stored in the terrestrial biosphere over a relatively long time span, while in the oceans it is exchanged and degraded faster, C storage in the terrestrial biosphere is essential to the attempts of increasing global C storage as well as in reducing degradation of land with high C stocks.

The role of the ocean-atmosphere flux is an important factor considering future changes in the atmospheric C pool. Since most of the oceans' C is recycled within the surface layer, but only small amounts are stored for several hundred years in deep ocean layers, processes like changes in ocean circulation need to be investigated further. Additionally, oceans represent the biggest CO_2 sink, reaching -2.2 ± 0.4 GtC yr^{-1} in the 1990s and -2.2 ± 0.5 GtC yr^{-1} from 2000-2005. About half as much is stored in terrestrial biosphere: -1.0 ± 0.6 GtC yr^{-1} in the 1990s and -0.9 ± 0.6 GtC yr^{-1} from 2000-2005 (IPCC 2007b). Regarding land use changes, global forests do not regrow as fast as deforestation is proceeding and already, the emissions due to land use change amount 1.6 GtC yr^{-1} in the 1990s (IPCC 2007b). This implies that C is taken up somewhere else in the terrestrial ecosystem. Several studies (IPCC 2007b; Stephens et al. 2007) suggest that this sink might be in forests. Firstly, because the C stock of tropical forests has been underestimated so far, and secondly, the increased C concentration in the atmosphere itself could have a stimulating effect on forest growth by increasing photosynthesis activity (Malhi & Wright 2004). However, at the same time it is possible that rising temperatures increase respiration and decrease water availability. Furthermore, CO_2 uptake could be restricted by nutrient deficiency or constrained by light competition (Körner 2004).

The fluxes between atmosphere, land and ocean are more or less in balance along a timespan of several years, whereas they may vary from one year to the next. Especially the fluxes of soil C, including weathering of rocks, are important for the global C balance on the long term (IPCC 2007b). Since pre-industrial times, the C concentration has been linearly increasing, from 280 to 380 ppm in 2010 (Fig. 2, left) (NOAA-Research 2012; Nieder & Benbi 2008), hence, the global C cycle is not balanced. Not only atmospheric CO_2 concentrations but also other direct GHGs as methane (CH_4), nitrous oxide (N_2O), perfluorocarbons (PFCs), hydrofluorocarbons (HFCs) and sulphur hexafluoride (SF_6) are increasing. Greenhouse gases absorb and emit solar radiation, which causes the atmosphere to warm up. Without natural GHG such as water vapour (H_2O), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and ozone (O_3), the earth's temperature would be approximately 30 °C colder than at present. A further increase in GHG concentrations, however, may lead to disastrous consequences for humanity.

Consequently, it is not surprising that the temperature anomaly increased (Fig. 2, right). Since the 1970s land and ocean temperatures have increased by 0.6°C (Hansen et al. 2012). A fact that cannot only be explained by natural causes such as the Milankovitch cycle, describing changes of the earth' orbit (IPCC 2007b). The C cycle gained specific attention because rising temperatures are attributable to the increase in C concentrations from pre-industrial times until today for about 60% (Grace 2004).



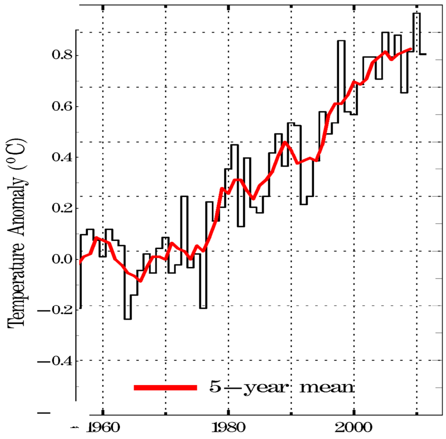


Fig. 2. **Left**: CO_2 concentrations from sites in the SIO Air Sampling Network in ppmv from 1960 – 2010 at Mauna Lao, Hawaii (Keeling et al. 2009). **Right**: Global temperature anomalies from 1880-2011 (land meteorological stations only). Modified from J.E. Hansen, R. Ruedy, M. Sato, and K. Lo; NASA Goddard Institute for Space Studies (Hansen et al. 2012).

After pre-industrial times the proportion of the C-13 isotopes in the atmosphere has declined. As this isotope is more abundant in the oceans and volcanic or geothermal emissions, it leads to the conclusion that the additional C originates from fossil fuel combustion and vegetation (IPCC 2007b). Continued burning of fossil fuels has the most severe effect on the global C cycle as a consequence of increased atmospheric CO_2 concentrations. CO_2 is the most voluminous GHG based on human-induced emissions (Gorte 2009), accounting for 75% of anthropogenic emissions. These increased from 5.4 ± 0.4 GtC yr^{-1} in the 1980s to 6.4 ± 0.4 GtC yr^{-1} in the 1990s and to 7.2 ± 0.3 GtC yr^{-1} from 2000-2005 (Marland et al. 2006). Moreover, due to the on-going disturbance of natural ecosystems, including deforestation, and land use change (1.6 GtC yr^{-1}, Fig.1) the human-caused emissions have exceeded the natural capacity to keep the C cycle balanced (Malhi 2002; IPCC 2007). According to Hougthon (2008) emissions from land to atmosphere averaged 1.5 PgC yr^{-1} in the 1980s, 1.56 PgC yr^{-1} in the 1990s and declined to 1.47 PgC yr^{-1} from 2000-2005.

In order to mitigate possible adverse impacts of climate change on nature and society, investigations are undertaken to achieve a better understanding of the factors that influence the C cycle as well as CO_2 storage. One of these investigations addresses the forest C cycle.

2.2. Forest carbon sequestration

Forests cover about 31% of the earth's land area, corresponding to about 4 billion hectares (FAO 2011). The smallest fraction has temperate forests, covering only 5%. Boreal forests cover about 11% and tropical forests 15% (Lorenz & Lal 2010). More than half of the total forest area can be attributed to only five countries: Russia, Brazil, Canada, the United States of America and China (FAO 2011). Deforestation declined from 16 million ha yr^{-1} in the 1990s to 13 million ha yr^{-1} from 2000-2010 (FAO 2011), even though it is still exceeding afforestation efforts (IPCC 2007b). Main deforestation activities occur in the tropical regions, while afforestation primarily takes place in the temperate and boreal zones. South America and Africa have the largest deforestation and lowest afforestation rate, losing 4 million ha yr^{-1} and 3.4 million ha yr^{-1} during 2000-2010, respectively. During the same time period, forests in Europe and Asia were expanding. Especially China carries out large afforestation measures (FAO 2010). These areas, however, consist mainly of plantation forests. In whole East Asia, these forests account for up to 35% of their total forest area, followed by Europe (excluding Russia) with 27%. In a global perspective, 7% constitute planted forests and 36% primary forests. More and more forests are included in management plans, with a trend towards sustainable forest management (FAO 2010). By now, 2/3 of the world's forests are under a national forests programme (FAO 2011). Since forests provide multiple environmental services, it is difficult to designate forests for one specific use. About 24% of all forests provide a "multiple use", meaning that their management considers a combination of several environmental services, e.g. protection of soil and water, production of goods, provision of social services and conservation of biological diversity. Yet, forests (30%) are predominantly used for production of wood and other forest products, the remaining are mainly subject to one function (e.g. conservation of biodiversity) (FAO 2010).

Regarding the C stock of forests, not only the different forest biomes essentially impact the potential C storage, but also different management practices (Gorte 2009; Lorenz & Lal 2010; Dixon et al. 1994; Apps & Price 1996) All forest ecosystems sequester C by the uptake of atmospheric CO_2 via photosynthesis (Fig. 3).

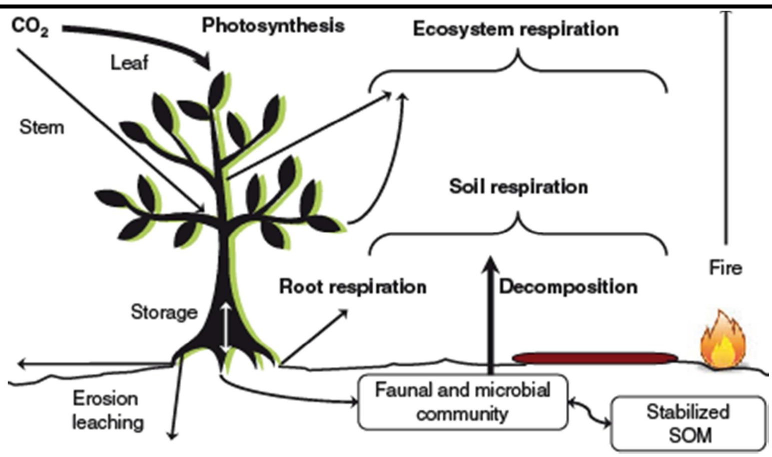


Fig. 3. Carbon cycle within the forest ecosystem (Lorenz & Lal 2010).

The sequestered C is mainly bound as organic compounds in plant tissue, detritus (accumulating on the forest floor) and soil. It accumulates in the soil via root growth and as decomposition product of dead organic matter via microorganisms (Gorte 2009). Though, the process of C storage is dynamic as the amount of C that is converted into biomass and transferred to the detritus and soil pools varies with tree species, age, growth pattern and other local conditions (Gorte 2009, Lorenz & Lal 2010). In addition, temporal changes of the C stock depend on disturbances and stand development, including canopy cover and stand age. These factors cause significant changes in the microenvironment, e.g. the intensity of radiation, the amount of precipitation that reaches the forest floor. Eventually, this results in changes in the nutrient availability and thereby in return effecting biomass accumulation (Apps & Price 1996).

Forests present a paramount importance to the global C cycle since they store about half of the total terrestrial C (Nieder & Benbi 2008). Boreal forests represent the greatest share in terrestrial C stock, containing 26%. Temperate forests account only for 7%, while the C stock in tropical forests amounts to 20% of the terrestrial C stock (Nieder & Benbi 2008). As stated in the Global Forest Resource Assessment Report (FAO 2010), the C stock in the world's forest ecosystem amounts to 162 t ha^{-1} in 2010, of which 45% were stored in forests soils, closely followed by biomass C stock with 44% of total forest C stock. Dead wood and forest floor C constitute 11% (Tab.1). In forests, up to 80% of all aboveground C and 40% of all belowground C is stored (Dixon et al. 1994). The ratio of soil and biomass C varies between forest biomes. Temperate forests, such as those in Europe, store two-thirds of total forest C in soils, while the soil C stock of boreal forests is 5 times higher than its biomass C stock. Tropical forests depict a one to one ratio of soil and biomass C pool (Dixon et al. 1994; FAO 2010; Lorenz & Lal 2010). As this study uses data from Denmark, the further focus lies on temperate forests.

Tab. 1. Forest carbon stock in t ha^{-1} by region, in 2010 (modified from FAO 2010).

Region	Carbon in biomass	Carbon in dead wood and forest floor	Carbon in soil	Total carbon stock
Africa	82.8	11.7	51.1	146
Asia	60.2	5.8	59.6	126
Europe	44.8	20.5	96.4	162
North and Central America	56.1	38.2	58.4	153
Oceania	54.8	15.3	43.2	113
South America	118	11.6	87.3	217
World	71.6	17.8	72.3	162

2.3. Carbon dynamics in temperate forests

Temperate forests cover approximately 10.4 million km^2, which is about 25% of the global forests (Dixon et al. 1994). They represent an estimated C sink of 0.2-0.4 Pg C yr^{-1} (Tyrrell et al. 2012). Regarding aboveground biomass C, most of it is accumulated in tree stems, less in tree foliage. The tree foliage shows by far the biggest C flux within the aboveground biomass, which is due to the process of photosynthesis (17.3 t ha^{-1} yr^{-1}). Furthermore, a considerable amount is transported to the roots (8.28 t ha^{-1} yr^{-1}). Belowground, C accumulates most in soil organic matter (SOM), followed by coarse roots. The fluxes belowground derive mainly from autotrophic respiration (7.82 t ha^{-1} yr^{-1}) (Malhi et al. 1999). However, with a shifting balance of photosynthesis and respiration rates, temperate forests might become a C source. This also depends on their resilience to disturbances, which mainly derive from humans (Tyrrell et al. 2012). Temperate forests are highly seasonal. Their growth and hence the productivity mainly depends on light and temperature (Malhi et al. 1999). Additionally, there is a high variability in C uptake within different stand structures (addressing age and disturbance for instance). While younger stands sequester more C than older stands, because they grow faster and their photosynthesis rate exceeds their respiration level, older stands contain (2-5 times) more C in total, which is due to the longer accumulation period (Jandl et al. 2007; Tyrrell et al. 2012). Carbon sequestration peaks in 11-30 year old stand classes (Tyrrell et al. 2012). As most temperate forests are N-limited, elevated N concentrations have a fertilizing effect on forest growth, at least until the saturation point has been reached. The same effect is observed by increased CO_2 concentrations (Malhi et al. 1999). Overall, the C storage process is influenced by several factors.

2.4. Factors influencing forest C storage

Carbon storage in general depends on the balance between photosynthesis, autotrophic respiration and heterotrophic respiration (Fig. 3). These factors in turn are affected by the length of the growing season, fire, drought, wind and ice, insects, N, ozone, as well as forest management and land use. Also the interaction of those variables should not be disregarded, though they are poorly understood. An early starting growing season can result in early bug breaks and an early end of the winter dormancy in conifers, thus increasing the C uptake in spring (Tyrrell et al. 2012).

A **fire** event leads to direct CO_2 release to the atmosphere through combustion. Carbon is also lost due to increased decomposition rates of the burned area and reduced biomass of the regenerated area (Tyrrell et al. 2012). In addition, depending on the frequency and magnitude, fire outbreaks promote bigger areas of younger forests with lower C stocks. Notwithstanding that, fire may cause soil C to increase (Lal 2005), which can be attributed to the incorporation of charcoal (Jandl et al. 2007). **Drought** events have a major influence on forest C storage since water is the predominant factor controlling tree growth as well as tree species distribution and therefore forest composition (Tyrrell et al. 2012; Lal 2005). Though, water limitation leads to a reduction of decomposition of soil C. Particularly **wind** storms affect forest succession phases. Generally, storms do not result in big C losses as long as the downed trees or branches remain on the ground (Jandl et al. 2007). Hence, the biomass C pool decreases, while the dead wood C pool as well as the forest floor C stock increase.

In **N**-limited forest types, N deposition increases tree growth and C uptake as well as decreases CO_2 emissions (Lal 2005; Jandl et al. 2007) due to declined soil respiration, at least in the short-term (Tyrrell et al. 2012). As N becomes directly available, the demand for recalcitrant N forms is reduced and consequently, lowers the soil respiration (Bowden et al. 2000). In contrast, the fertilization effect of N on N-limited forest sites is controlled by the specific site conditions (mainly soil processes). Thus, it does not necessarily lead to an increased C uptake, but could also decrease the soil C content when N additions cause root biomass to decline (Jandl et al. 2007). Moreover, high ozone levels diminish tree growth especially in conifers by injuring foliar, subsequently, reducing C sequestration. High ozone levels occur in areas with high levels of sun radiation and fossil fuel emissions (Tyrrell et al. 2012).

In addition to those abiotic disturbances, **insects**, particularly defoliating insects, can alter the C sequestration rates in forests by increasing the mortality rate of with widespread defoliation. Although, this has just a slight effect on net ecosystem productivity (Tyrrell et al. 2012). Though, increased litter fall and accompanied changes in C:N ratio, photosynthesis and decomposition rate through defoliation may affect nutrient cycling. Increased mortality result in a shift of C from biomass pool to dead wood pool as well as overall decreasing photosynthesis rates but increasing decomposition rates and consequently in a higher soil C stock (Tyrrell et al. 2012).

Finally, the forest **management** affects C sequestration and storage. Management for timber harvesting, for instance, includes various rotation phases where C is released at the initial phase and later on, sequestered again. Beyond the harvesting, the gained wood products still contain stored C. The turnover time, however, varies by product. Wooden building structures have far longer turnover times than paper for example (Tyrrell et al. 2012).

More importantly, some of the above mentioned factors are also influenced by climate variables, mainly temperature and precipitation. Within the tree, C is assimilated in the chloroplasts where the photosynthetic reaction takes place and the assimilated C is further transported to sites where it is needed for consumption or the formation of plant tissues. These sites appear in foliage and stem as well as in reproductive materials (inflorescences, fruits/seeds, nectar) and in roots (Lorenz & Rattan Lal 2010). In addition, C is also exported to soil microorganisms and mycorrhiza. Further, it is lost from the tree biomass through leaching in form of dissolved C to the soil.

Already in the **chloroplasts**, C_3 plants respire about 20-40% of the photosynthetically fixed C through photorespiration. Additionally, the process of creating sugar for the Calvin cycle leads to CO_2 respiration. Furthermore, CO_2 is also released by mitochondria during plant leaf and root respiration for maintenance, synthesis and growth, which is correlated to photosynthesis rates. In general, maintenance respiration rises with increasing stand age of trees and about 25% more C is released through growth respiration than is sequestered in new tissues. In total, about half of the absorbed CO_2 in temperate forests is released to the atmosphere (Lorenz & Lal 2010). The optimal temperature for photosynthesis in trees is between 5 and 25°C. Most C is taken up in spring and early summer. Although high temperatures during this time enhance C uptake, it is decreased when high temperatures continue during summer or occur at the end of the growing season (Malhi et al. 1999).

Young **leaves** that have not yet reached 25% of its full size are C sinks, taking up C from photosynthesis and older leaves. Older leaves, instead, are C sources, exporting C to other parts within the tree (Lorenz & Lal 2010). During the whole life span of a tree, **stem** wood represents the largest C stock. With continued age, sapwood in the inner part of the tree is converted to hardwood which has a higher wood density and thus higher C content (CRFR. n.d.). In general, gymnosperms (coniferous trees) contain lower wood densities than angiosperms (broad-leaved trees), varying with the height within the tree as well as within individuals (Jandl et al. 2007). Annual trees belong to r-strategists meaning that they have a short generation time and a high reproduction rate relative to K-strategists. Hence they partition more C to reproductive organs than perennials (Lorenz & Lal 2010). About 50% of the aboveground stored C is allocated to the belowground biomass. As Ericsson et al. (1996) indicates, C limitation in trees causes **root** growth to decrease, no matter if the C shortage is a consequence of reduced photosynthesis rates or of competition between root growth and ammonium uptake. The same effect is reached due to competition from intensive shoot growth and with low soil temperatures. Furthermore, tree roots can become a C source within the tree, for instance in spring growth. Dead roots display a source of C for the decomposition of litter or act as a substrate for litter decomposition, whereas living roots release C to the soil by various processes, e.g. through root-associated symbionts or respiration (Lorenz & Lal 2010). Root respiration varies with soil temperature. Generally, C release by roots is higher in forest floor than in the soil independent of the temperature, as root tissues in the forest floor have higher nutrient concentrations (Tyrrell et al. 2012). It has to be taken into consideration that the difference between forest floor and soil is not always clearly detectable.

Outside the tree, the litter input, decomposition rate and SOM content determine the C flow to soil microorganisms and mycorrhiza. **Litter** input depends on the normal senescence process and seasonal fall off of vegetative and reproductive parts. Besides this, also natural disturbances such as fire, wind, ice, snow and heavy rainfall in form of e.g. hail contribute to litter input to forest floor and the soil. While plant residues constitute the main substrate for **decomposition** and thus, make up the highest share (about 70-80% are derived from litter (Baritz et al. 2010)) of soil organic carbon (SOC) content, microbial biomass represents only about 5% of SOC (Lorenz & Lal 2010). Decomposition of litter and consequently of the decomposer's respiration rate is controlled by plant specific litter properties (e.g. C/N ratio), by physical and chemical properties of the surroundings (soil temperature, soil moisture), by the composition of the decomposer community (Horwath n.d.) and by nutrient availability (Tyrrell et al. 2012). For instance, high lignin or tannin contents reduce the speed of litter decomposition. Moreover, prolonged water-saturation of the top soils induces slower decomposition rates (Baritz et al. 2010). In contrast to the formation of SOM, where C is reassembled in new molecules, the mineralization process leads to C release in form of CO_2 and CH_4 due to heterotrophic activities (Lorenz & Lal 2010). The heterotrophic activity is positively correlated with temperature, resulting in decreasing residence time of SOC (Tyrrell et al. 2012).

At the initial stage of decomposition, organic material (of plants, microbes and animal residues) is leached by water and either absorbed to SOM (Raich & Nadelhoffer 1989) or taken up by soil organisms or lost as dissolved organic carbon (DOC) (Lorenz & Lal 2010). Further, the soil macro- and mesofauna carry out litter fragmentation by feeding on detritus, as well as transport litter fragments deeper into the soil. What is more, they affect the litter quality by altering the chemical compounds of detrital C within their digestive system, making litter organic matter more stable to further decomposition. The microfauna further decompose the remaining detritus. In comparison to bacteria, fungi dominate the decomposition process. Fungi can perform at lower pH than bacteria. Additionally, soil food webs that mainly constitute of fungi have higher SOM concentrations compared to those dominated by bacteria. Since the different decomposition phases occur with different speed, the litter pool may be over- or under-estimated, using short- or long-term decomposition rates respectively (Lorenz & Lal 2010). In addition to decomposition processes in litter and soil layers, it also takes place in standing dead wood. The SOM derived from coarse woody debris is more stable to decomposition than that of litter. In general, gymnosperm wood decomposes slower than angiosperm wood because the wood is less dense, has a higher lignin content, lower N and P concentrations and a higher lignin:N ratio. While a relationship between decomposition rate of angiosperm wood and N & P concentrations (faster) as well as C:N ratios (slower) has been observed, gymnosperms do not show such a correlation (Lorenz & Lal 2010). The slowest decomposition rate and thus a stable C content in the long-term, is in passive SOM pool with a turnover time of 100 to >1,000 years. The labile compounds are already degraded in the first decomposition phases, leaving more recalcitrant compounds with every further degradation step. However, the turnover rate depends on soil properties (e.g. texture, moisture, pH), site conditions and C composition (Silver & Miya 2001). Its accumulation is encouraged in low temperate and low oxygen-containing soils. On the whole, deeper soil layers contain relatively more stabilized and recalcitrant C than upper layers. Nevertheless, increased amounts of C from roots leaching in the soil show a stimulating effect on decomposer activity, hence enabling further decomposition of SOC in deeper layers resulting in a loss of ancient buried C (Lorenz & Lal 2010).

Last but not least, **leaching** of dissolved C is a further component of C dynamics in forests. Deciduous trees are more susceptible to leaching than conifer trees. More C leaches from older leaves than from younger ones (Lorenz & Lal 2010). In addition, trees emit biogenic volatile organic compounds (BVOC) and VOC compounds as well as CH_4 and CO, although at far lower magnitude than CO_2. BVOC emissions (e.g. isoprene) increase with increasing temperatures, having a protective function, but are inhibited with elevated CO_2 concentrations (Lorenz & Lal

2010). In case if trees are beetle-infested they release up to 20% more VOC compounds as healthy trees to defend against them (Amin et al. 2012).

Biomass carbon stock

Regarding aboveground biomass, the tree species composition is an important factor for the C sequestration potential. In comparison to stands with a similar age structure, beech and Douglas-fir stands consist of a higher aboveground C stock. Forests with a mixed-species stand contain more C than single species stands (Tyrrell et al. 2012). On the one hand, an explanation would be that in a mixed species stand, the characteristics of the tree species complement each other enabling the stand at a whole to a more efficient resource use. On the other hand this effect can be explained by a facilitation effect between different species. According to this, one species might increase the nutrient availability for others due to its relatively nutrient rich litter (Tyrrell et al. 2012).

In general, the C allocation of trees to belowground biomass is lower than in aboveground biomass, but highest on dry sites, whereas the stand age shows no effect on the aboveground-to-belowground biomass proportion (Tyrrell et al. 2012).

Dead wood carbon stock

In general, more dead wood is accumulated in unmanaged than in managed forests, albeit the amount also depends on the natural mortality rate and the decay rate. In addition, the frequency and severity of disturbances through e.g. extreme weather events plays a major role in the proportion of dead wood in a forest. Especially after disturbances, dead wood constitutes an important share in the total forest C stock by offsetting the C loss in the biomass pool (Mäkipaä et al. 2008). Woody debris can contain large amounts of C and store it for a longer time due to slow decomposition (Tyrrell et al. 2012).

Forest floor carbon stock

The litter quantity and quality varies with tree species and hence for forest types (Lorenz & Lal 2010; Jandl et al. 2007; Currie et al. 2003). In deciduous forests, litter accumulates during the winter season as it decomposes slowly, and diminishes quickly in the growing season. In comparison to coniferous forests, deciduous forests receive larger litter fall. However, the litter layer is higher in coniferous forests. Since coniferous litter has higher lignin content, it decomposes slower. Nevertheless, the C pool is similar in both forest types (Tyrrell et al. 2012). Decomposing of litter results in emission of CO_2 to the atmosphere as well as in further distribution to the soil in form of organic compounds (Tyrrell et al. 2012). Under given conditions of dryness and older stands, the litter C pool constitutes to about 10% of the total C stock (Tyrrell et al. 2012). Moreover, environmental changes such as alterations in tree species composition (which contradict the notation of Tyrrell et al. 2012) cause rapid changes in the forest floor layer (Baritz et al. 2010; Currie et al. 2003). All in all, this pool is highly variable due to its rapid turnover times.

Soil carbon stock

The soil C stock accumulates depending on climatic conditions (e.g. precipitation), soil type, turnover rates of fine roots, leaching, decomposition rate as well as input rate of litter and SOM, perturbations (Raich & Nadelhoffer 1989; Lal 2005), and activity of arthropods (Lorenz & Lal

2010). The latter are mixing litter and soil and thereby, affecting the soil C pool both positively and negatively. Positive effects are gained by the mixing of soil into deeper layers. A negative aspect of this could be that deeper soil layers, containing recalcitrant C pools, are exposed to greater mineralization when brought to the upper soil layers. Therefore, rapid decomposition of litter due to high arthropod activity can result in declining soil C stock and higher soil respiration rates. As part of the SOM, the root mortality and decomposition varies with soil type and influences the soil C stock (Silver & Miya 2001; Jandl et al. 2007). The root distribution and thus the incorporation of C in the mineral soil also depends on tree species (Vesterdal et al. 2008). As in general, the root system is rather shallow and widespread, by far the main portion (90-99%) of the root system is found within a soil depth of down to 1 m (Crown 2005). Thus, the main C fluxes from tree to soil occur in the top 1 m. In combination with this, the microbial activity and hence decomposition rate is highest within the same soil depth. Moreover, root respiration contributes a major part to total soil respiration (Raich & Nadelhoffer 1989). According to Crown (2005), roots in coarse textured soils penetrate to a greater depth than those in loamy or organic rich soils. However, besides the species-specific root system, high bulk density e.g. in fine sandy soils and compacted clay soils, constrains the rooting depth. Further, low oxygen availability and high moisture content inhibit root growth, whereas organic-rich fertile soils enable root proliferation (Crown 2005; Coder 1998).

Degradation and mineralisation processes and thereby soil respiration are dependent on climate variables, such as temperature and precipitation, composition of the microorganism community and nutrient availability. It is generally higher under warm or moist conditions. Additionally, the magnitude of soil disturbance also affects the overall soil C pool (Tyrrell et al. 2012). Baritz et al. (2010) indicates that coarse texture soils, like sandy soils, store C differently than fine textured soils. Fine textured soils are expected to have higher C stocks because of their high litter and root production as well as an active decomposer system (Baritz et al. 2010; Lal 2005). Furthermore, as Baritz et al. (2010) suggests, parental material influences C stock of soils since soils developed on calcareous parent material store significantly more C than non-calcareous soils.

Stand age and forests with similar land use history, however, do not influence soil C stock (Tyrrell et al. 2012; Jandl et al. 2007). In order to compare study results, soil C surveys are undertaken up to 1m depth. Yet, studies indicate that in addition to the upper 1m, deep mineral soil (1-9m) also has a relatively large and stable C stock. As a consequence, the soil C stock might still be underestimated (Tyrrell et al. 2012).

The forest floor and soil C pool are linked since DOC leaches from the upper layers to the mineral soil (Currie et al. 2003; Vesterdal et al. 2008). On the whole, soil C stocks are less influenced by temperature and moisture, disturbances, changed management practices and tree species composition as it is the case for forest floor C stock (Currie et al. 2003), but more by constant factors e.g. climatic zone, texture or elevation (Baritz et al. 2010). However, generally, soil disturbance leads to net soil C losses (Jandl et al. 2007). On the one hand, soil disturbances cause changes in microclimate which in turn stimulate the decomposition of SOM and lead to soil C losses. On the other hand, water infiltration is improved and roots might have better development conditions, thus displaying a C input (Jandl et al. 2007).

Forests are not only of significant importance to the global C cycle in terms of C sequestration, but also because of their reaction to changing climatic conditions which in turn affects the forest

C stock in total as well as in its different pools. Magnani et al. (2007) demonstrated that at least the C cycle in boreal and temperate forests is directly or indirectly influenced by humans due to forest management or N deposition. As trees have a relatively high longevity and therefore cannot easily adapt to rapid changes in climate conditions, forests are quite sensitive to climate change (Lindner et al. 2008). Moreover, species that are better adapted to certain climate conditions cannot migrate fast enough to replace those that cannot stand the alterations and have stopped to reproduce (Sedjo & Sohngen 1998).

2.5. Climate change impacts on forest ecosystems

Climate change will have both negative and positive effects on C sequestration in forests. They have to adapt to changes in mean temperature, combined with an atmospheric CO_2 increase and precipitation as well as to an increased variability of conditions. In addition to this, they also have to adjust to extreme weather events such as droughts, storms and floods as well as their changed frequency and duration (Lindner et al. 2010). Since there are different climate change scenarios, the impact on forests might vary (IPCC 2007a; Lindner et al. 2008). For instance, global temperature is predicted to increase within a range of 1.8°C to 4°C by 2100 compared to 1990. Furthermore, precipitation pattern will differ, depending on e.g. topography and vegetation. All in all, these changes and the kind of impact vary between seasons and regions and its different site conditions.

In general, all these changes will affect the (a) forest area extent, (b) biodiversity comprising competition between species, (c) health and vitality including resistance to pest and disease outbreaks, tree growth, productivity and changes in damage by natural disturbances such as fire or storms, and (d) ecosystem services. However, boreal, temperate or tropical forests show a different vulnerability (FAO 2012; Lorenz & Lal 2010; Lindner et al. 2008).

(a) Forest area

The total forest area is expected to be affected by changes in temperature and precipitation, species composition including biological diversity, and more frequent and more intense natural disturbances. The forest area extent, though, is expected to increase in temperate regions, whereas it will contract in boreal and tropical regions (Lindner et al. 2008).

(b) Biodiversity

Whether species survive and grow is largely dependent on climate variables and the species specific tolerance to changes in living conditions. Most species show their highest growth rate, competitive strength and robustness to disturbances, pests and diseases best under specific optimal conditions. Thus, some species adapt better to changing climate than others, hence they displace others, causing a shift in biological diversity with a possible dominance of invasive species (Lucier et al. 2009). Above all, besides the geological aspect, temperature and precipitation wield the greatest influence on species distribution and composition (Whittaker 1967 in Breshears et al. 2008). The growing season is longer and might start earlier leading to an earlier bud break for some species, changing time in flowering, pollination and litter fall. Consequently, productivity and C sequestration rates are changing (FAO 2012). Earlier bud break affects the amount of radiation reaching the forest floor, influencing the microclimate, whereas litter fall affects the soil C content (Breshears et al. 2008). According to Chapin III (2003) (in Breshears et al. 2008), deciduous-dominated forests have a lower proportion of incoming radiation than conifer forests.

(c) Health and vitality

Atmospheric CO_2 acts as a fertilizer (Lal 2005) because photosynthesis rates increase with elevated concentrations of this GHG, depending on the plant N status and the species (Norby et al. 1999). Deciduous tree species respond to raised CO_2 more than conifer species as a short-term study of Ceulemans & Mousseau (1994) shows. Contrary to this, Norby et al. (1999) discovered in long-term studies that unstressed conifers have a more similar response than deciduous trees. However, tree growth is not proportionally linked to increased photosynthesis activity, hence other factors like nutrient availability create a limiting effect on growth rates (Körner 2003). For instance, the demand for N increases with increasing CO_2 (Luo et al. 2004). Moreover, increased atmospheric CO_2 is beneficial for the plants' water use efficiency: stomata are partially closed and thus, less water is lost through transpiration (Picon et al. 1996). Contrary, transpiration results in a cooling effect, so that with raising temperature, the positive effects on water use efficiency may be reversed, e.g. respiration rates of most European tree species increase and photosynthesis is impeded if the temperature exceeds 30°C (Rennenberg et al. 2006). In contrast to C_3 plants, C_4 plants have solved the problem of water loss through stomata while performing photosynthesis at higher temperatures. Here, CO_2 concentrations are higher at the site of the Calvin cycle where the stomata do not necessarily have to open (Lorenz & Lal 2010). Alongside with an increased CO_2 uptake, C allocation to root growth increases, allowing trees to take up soil water in deeper soil layers and therefore improving their adaptation to water-limited environments (Wullschleger et al. 2002).

Since increased CO_2 concentrations are coupled with increasing temperature, temperature is expected to stimulate tree growth and extend the growing season. However, only increased temperature alone only has a positive impact on boreal and temperate forests (Lindner et al. 2008). In combination with other factors, e.g. water availability, the response of forests may be adverse (droughts). Furthermore, warmer temperatures lead to enhanced availability of mineral N for plant uptake (Lal 2005). In addition to CO_2 and temperature, also precipitation affects photosynthesis rates. In areas where tree growth is water limited, increased rainfall causes higher productivity as Kirschbaum (2004) describes (in Lindner et al. 2008). Once trees are saturated, production will not further increase (FAO 2012). Another effect accompanied with climate change displays increased cloudiness, resulting in reduced sun radiation, which can lead to some extent to a decrease in net primary production (Melillo et al. 1993). Finally, precipitation and temperature also affect forest soils. Litter is decomposing faster, releasing SOC and the residence time of nutrients is shortened with increasing temperatures and moisture (Townsend & Rastetter 1996; Lensing & Wise 2007; Rennenberg et al. 2006).

Forests are not only directly influenced by increasing temperatures but also indirectly through growing insect populations, that benefit from elevated temperatures (Lindner et al. 2010; Lucier et al. 2009; Tyrrell et al. 2012). On the one hand, mortality of herbivore and pathogen population during winter decreases with global warming, whereas on the other hand, raising temperatures in the tropics lead to a shortened life span of pathogens. Additionally, pest species might expand to other forests (northwards). Beside climate, the resistance also depends on tree species and stand age (Lucier et al. 2009) as well as plant nutritional quality and community interaction, e.g. host-parasitoid balance (Lindner et al. 2008).

Moreover, increasing temperatures accompanied with water shortage, amplify the risk of fires (Lindner et al. 2008; IPCC 2007a). As a result, organic matter is removed and nutrients are lost due to e.g. leaching and volatilisation. This does not happen without affecting the C stock. The caused damage in turn makes trees more susceptible to insects and pathogens (Lucier et al. 2009). The same is true for damages caused by windthrow, storm and flooding. Extreme flooding events have a severe effect on forest health during the growing season. Beside injuries, the mortality and senescence is higher and the production of seeds is inhibited (Glenz et al. 2006 in Lindner et al. 2008).

(d) Ecosystem services

The way forests respond to climate change also affects its ecosystem services. As tree growth benefits from increased atmospheric CO_2 and warmer temperatures, the enhanced productivity is beneficial for timber harvesting. Accompanied with increasing productivity, the rate of C sequestration and storage of forests rises. However, in the long-run, increasing atmospheric CO_2 concentrations combined with longer drying seasons and increasing temperatures, are expected to turn forests in a C source instead of expanding the stored C pool or at least reduce the forest C sinks (FAO 2012). Other ecosystem services, such as soil and water protection largely depend on the regional variability of climate change concerning e.g. precipitation levels, extent of the dry season.

Overall, boreal and temperate forest biomes are expected to shift polewards, whereas tropical forests are likely to expand polewards. In general, there are high uncertainties in the predicted response of forests to climate change. Nevertheless, the northwards shift of boreal forests and higher temperatures result in changes of the species composition, e.g. in the southern regions of boreal forest biomes coniferous species are replaced by deciduous trees. In addition, thawing permafrost soil lead to increased microbial decomposition and thus, in a release of CH_4 and CO_2. All this is accompanied by insect invasions (e.g. bark beetles) to new areas and increased fire outbreaks. Even though elevated CO_2 accelerate tree growth and soil C stock, since the chemical changes in leaves due to altered CO_2 concentrations lead to slower decomposition, it does not offset the predicted C losses. Therefore, boreal forests are likely to become a significant C source (Lorenz & Lal 2010).

Temperate forests are less severely affected by climate change than other forest biomes. Generally, enhanced tree growth benefits C storage in biomass and soil. Carbon sequestration and storage occur at higher levels and for longer time periods in conifer dominated forests than in deciduous forests. Yet, increased CO_2 concentrations affect competitive interactions of tree species, which in turn affects decomposition rates and root production. A paramount importance is attributed to human induced disturbances (in terms of land use and forest management, e.g. addressing harvesting practices), with a potential to increase the total C stock of temperate forests (Lorenz & Lal 2010; Tyrrell et al. 2012).

The impact of climate change on tropical forest C pool is highly uncertain. Warmer temperatures will alter the rainfall pattern, causing the C sequestration in biomass to decrease with heavier rainfalls. In addition, plant respiration is increased and likely to offset C storage due to enhanced tree growth. Moreover, the risk of disturbances through fire is amplified not only by more drought events but also by human induced disturbances (Lorenz & Lal 2010).

Net C storage in forests implies that the sequestration of C is higher than the amount of C emitted by forests through respiration and removed by harvest. Hence, it is of major interest to understand the storage processes in forests, as well as its influencing factors. If so, it is possible to increase the C sink in each forest type as long as the maximum C stock is not reached yet. This in turn, results in a reduction of the rate at which global temperature is rising. In order to strengthen the adaptive capacity and diminish the vulnerability, the most efficient measure comprises to maintain forest areas and support biodiversity. Old and damaged trees should be removed in order to reduce the risk of pest outbreaks (FAO 2012; Nieder & Benbi 2008). However, using forests as a climate change mitigation tool can only be a supplementary option, while the overall reduction of C emissions from fossil fuels should be the major target (Nieder & Benbi 2008). There are constraints and limitations on the role of forests as a GHG mitigation tool.

2.6. Constraints on the role of forests in greenhouse gas mitigation

Besides its use for the national reporting, the data from NFIs may support elaboration of instructions for a more C friendly management of Danish forests e.g. advising to plant tree species that sequester more C than others. This may give rise to conflicts with supporting the regrowth with natural vegetation, as C often accumulates more slowly on areas left for natural vegetation regrowth than on planted stands with fast growing species. Basically, an increase in forest C sinks could be reached through increasing growth, afforestation, reforestation, regeneration, agroforestry and/or urban and community forestry (Apps & Price 1996; Dixon et al. 1994). The forest area does not necessarily have to extent but an increase in the growing stock (biomass) is sufficient in order to raise the total C stock (Karjalainen et al. 2002), albeit there are some major constraints to forest management practices that focus solely on C sequestration, including both ecological and geopolitical issues. First of all, high C uptake rates do not imply that much C is sequestered. Maximal C sequestration is obtained in younger stands because they are growing faster, whereas a maximum C storage rate is achieved in old forests or through extended rotation periods (Carroll et al. 2012). Secondly, as the C cycle and the influence of forests in this cycle are of global magnitude, all countries have to be involved in negotiations about the implementation of measures to reduce global warming. Nevertheless, these international responsibilities have to be reconciled with national interests (e.g. poverty alleviation). Further, it has to be considered that forests provide more services than C storage. These services encompass mostly positive effects on biodiversity, culture, society and economy not only at local but also on national and international levels (Steward & Maini 1996). Thus, the expansion of existing C sinks by limiting collection of fuelwood for instance, as suggested in (Dixon et al. 1994), is not always possible or desirable. Despite the urgent need to take joint actions, each state has its right for sovereignty, which has to be respected but could be met with well adapted compromises and /or subventions.

Besides the efforts of managing forests in a way that a maximum C sink is guaranteed, the future influence of forests to the global C cycle is also affected by the rate of deforestation especially in the tropics, which constitute the biggest C source of the global forest biomes (Lorenz & Lal 2010). Double the amount of C is released compared to the C forest sink as a consequence of tropical deforestation. The emissions not only derive from aboveground biomass, but also from SOC, since the turnover rate of fine roots as well as the allocation of C into the soil alters on clear cutted areas. Furthermore, deforestation of one area also affects the surrounded forest areas; increasing the sun radiation throughfall, leading to higher temperatures and risk of fire, hence changes in the microclimate and microbial activity, resulting in C release. In addition to tropical forests, both peatland forests and old-growth forests constitute a large share of the total terrestrial C sink (Lorenz & Lal 2010). Therefore, any perturbation could cause immense C emissions. Overall, unused forests show the greatest C sequestration potential, while selective cutting yields the best results in terms of C sequestration under management activities. This inevitably leads to conflicts with wood production (Fischlin 1996). Conflicts facing the maintenance or expansion of forest areas lie within expanding population accompanied with an increasing demand for natural resources, e.g. forest products, and land, causing deforestation and forest degradation (FAO 2012). Moreover, agricultural subsidies and the demand for renewable energy from corn and oil seeds, such as oil-palm plantations, make the conservation of forests more difficult.

While conducting studies to estimate forest C and to determine influencing factors, like in this study, the above mentioned constraints have to be considered in the final forest management strategy.

2.7. Danish forests

Denmark is aiming to further increase the forest area to 25% before 2100 (Christensen & Iversen 2004). In general, a conversion into e.g. croplands hardly occurs (Nielsen et al. 2011). However, some forests are cleared in order to transform the land to grassland or settlements. In 2002, the Danish National Forest Programme was put into force promoting a sustainable forest management, that encompasses a near-to-nature approach for forest management (Christensen & Iversen 2004). With the new guidelines, although voluntary, one seeks to achieve an improvement of forest biodiversity as well as forest economy. Additionally, those measures facilitate stakeholder participation and allow a more flexible management (Christensen & Iversen 2004). This appears central to Danish forest policy since most of the forest area (68%) is privately owned, whereas only 18.5% belongs to the state (Nord-Larsen et al. 2010).

According to Bradshaw et al. (1999) the natural forest composition today would be less diverse deciduous forest. Former species-rich deciduous forest types would have been replaced by *Fagus* dominated combinations. The Danish forests today are dominated by *Picea* (especially Norway Spruce) and *Pinus* along with *Fagus* (Bradshaw et al. 1999, Nord-Larsen et al. 2010) (Fig. 4). Pure conifer and broadleaf forests cover 41% and 39% of the whole forested land, respectively. Forests with a mixed proportion of broadleaves and conifers, with less than 75% of each type, account for 12%, Christmas tree plantations for 4 % and the remaining area is temporarily unstocked or unstocked (Nord-Larsen et al. 2010). Exotic species have become more widespread particularly due to plantation forestry (Bradshaw et al. 1999). About 66% of the forest area is managed as evenly aged plantation forest (Nord-Larsen et al. 2010). Yet, as a consequence of the new policies, more indigenous tree species have been planted and land has been afforested, so that the fraction of broadleaf forests is increasing (Eggertsson et al. n.d.). The near-to-nature management approach focuses on native species and mixed stands, and will therefore help to create forests that are ecologically more valuable. Additionally, these forests are more likely to withstand climatic changes because it is proved that the native species survived former changes in the climate during the history of earth (Bradshaw et al. 1999).

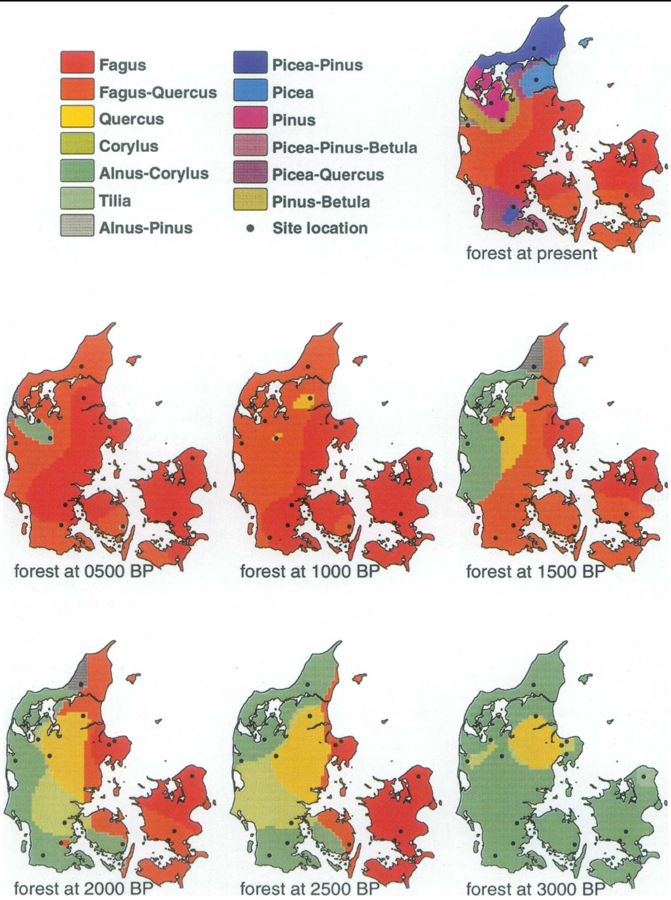


Fig. 4. Forest types occurring in Denmark at seven time-slices (Bradshaw et al. 1999).

3. Objectives and hypothesis

Objectives

The overall aim of this study is to explore which factors determine the size and distribution of the C pools in Danish forests, and to elaborate explaining models for the different absolute and relative pools.

More specifically we aim at estimating the absolute and relative C stock of the following four C pools within the forest ecosystem:

(1) biomass, including both above- and belowground biomass,

(2) dead wood,

(3) forest floor and

(4) soil.

Hypothesis

We generally expect:

- the largest C pool in the soil, on average being twice as big as the biomass C pool (Dixon et al. 1994; FAO 2010; Lorenz & Lal 2010), with forest floor and dead wood C pools holding a rather small share of the total C stock. However, the relation of soil and biomass C pool varies with different stand ages.

Moreover, we hypothesize that the absolute and relative C pools are related to:

- soil category (loamy, organic, sandy),
- tree species category (conifers, broadleaves, mixed, temporarily unstocked) as well as to some specific tree species (ash, beech, oak, fir, larch, Nordmann fir, Norway spruce, pine and Sitka spruce),
- stand age,
- crown cover,
- broadleaf fraction,
- tree species biodiversity (using the Simpson-Index),
- precipitation and
- previous land use (afforested areas (since 1990) and forests remaining forests).

We assumed that:

(1) for the **biomass** C stock especially the tree species category, the stand age and the crown cover will have a significant effect. The species effect is, however, confounded with the soil category to some extent as the properties of the soil gives the basic conditions for plants to grow and survive on that site. Stand age and crown cover is expected to be of significance for the biomass C pool because both are expressions of the C accumulation in trees (Jandl et al. 2007; Tyrrell et al. 2012). Nevertheless, a high crown cover does not necessarily include a high biomass C stock compared to areas with lower crown cover. A stand with a high crown cover can be composed of both only young trees and only older trees. Although the crown cover is high on both stands, the biomass C stock differs as younger trees contain less C than older trees (Carroll et al. 2012; Lorenz & Lal 2010).

(2) the **dead wood** C pool might not have a significant and representative effect of one of the explanatory variables, since there are only very few plots with dead wood content.

(3) the main explaining variable for **forest floor** C is tree species category (Vesterdal et al. 2008; Lorenz & Lal 2010; Tyrrell et al. 2012; Horwath n.d.). Previous land use is likely to affect the forest floor C stock, because the forest floor in recently afforested areas has not yet accumulated as much organic material and C as in forests existing for a longer time (Vesterdal et al. 2009; Jandl et al. 2007).

(4) the **soil** C stock is significantly influenced by the soil category (Silver & Miya 2001; Baritz et al. 2010; Lal 2005). In the short term, previous land use might also affect the soil C (Vesterdal et al. 2009; Jandl et al. 2007).

It is not clear which effect to expect of tree species biodiversity. It might, however, be displayed by significant differences between the tree categories, if for example plots consisting of mixed conifer and broadleaf forests have a bigger C pool in biomass or soil than those dominated by one of them.

4. Material and methods

4.1. Description of the study sites

Denmark is a northern European country, situated to the north of Germany between the northern and the Baltic Sea, at 56° N longitude and 13° E latitude, comprising an area of 43,098 km². The land is flat to undulating with an average altitude of 30 m above sea level and a maximum elevation of 173 m above sea level. It is characterized by a temperate climate with mild winters and cool summers, having an annual mean temperature ranging from 7.7 to 8.1 °C during the last 60 years. The annual mean precipitation ranges from 670 to 750 mm (Cappelen 2011). At the end of the Pleistocene, the glaciers decreased and the climate in Denmark has changed several times since that time. These factors influenced soil forming processes and contributed to present soil properties in Denmark. The country is divided into six landscapes that are differentiated by soil properties and/or parent material (Fig. 5). Denmark is dominated by a Weichselian moraine landscape with glacial sand, gravel as well as till. The western part of the country consists of deposits from the older Saale glaciation in form of sand and gravel which are surrounded by a Weichselian plain landscape with glacio-fluvial deposits. The northern area is composed of uplifted marine sediments from the Holocene that enclose a Weichselian marine core. West Denmark is fringed by dunes, which can also be found as inland deposits in central Jylland. Small parts in west and south-west Denmark present marsh landscapes consisting of mainly tidal sediments (Fig. 5) (Gravesen et al. 2004).

About 60% of the land is used for agricultural purposes, followed by forests as the second biggest land use. Since 1951, when forests made up 10 % of the country, the forested areas have slightly but steadily increased to 11% in 2000 (Levin & Normander 2008). More efforts have been made in the following years and the forest area comprises 13.5% (579,700 ha) in 2009 (Nord-Larsen et al. 2010) (Tab. 2).

Tab. 2. Forest area divided into land use classes (changed after Nord-Larsen et al. 2010).

	Total forested area	Conifer forests	Broadleaf forests	Mixed forest (conifer & broadleaf)	Christmas tree plantations	Temporarily unstocked	Unstocked
ha	580	235	229	72.2	23.8	12.0	7.91
%	13.5	40.5	39.5	12.5	4.1	2.1	1.3

The percentage of natural areas in the open land, including heathland, meadows and grasslands, has drastically decreased during the last decades. While in the late nineteenth century open natural and semi-natural habitat types covered about 25% of the total land area, it reaches only 9% in 2011. During the same period, build-up areas like roads and housing constructions have increased from about 3% to 10% (Levin & Normander 2008; Anon 2010).

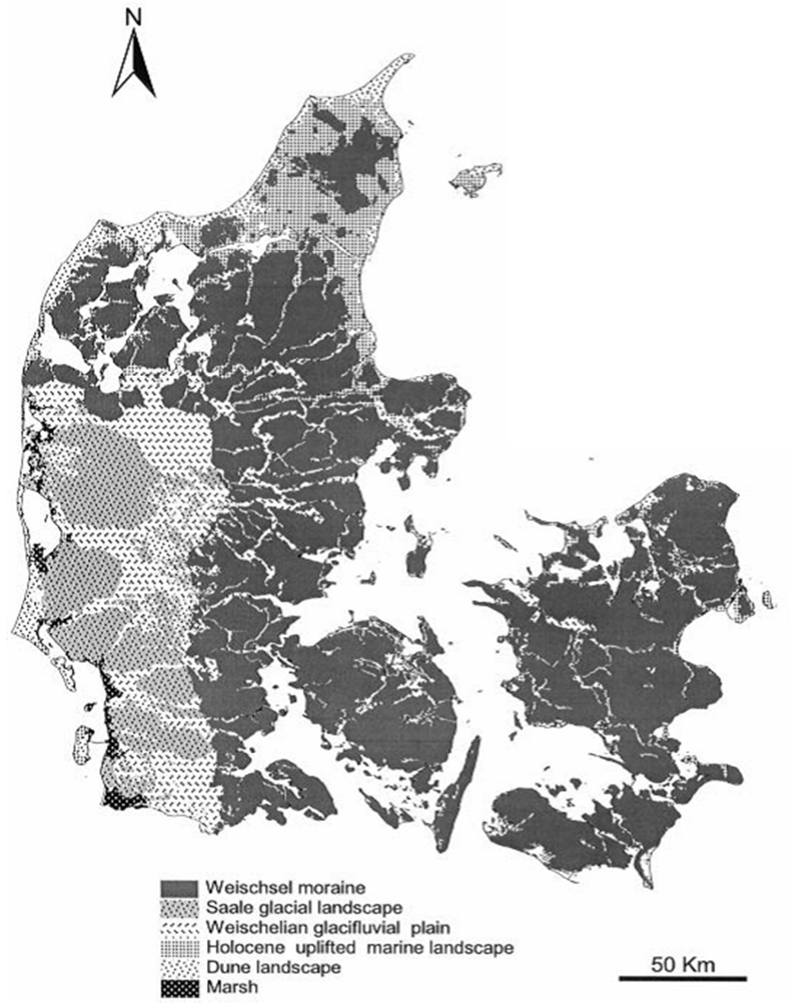


Fig. 5. Landscape types in Denmark (Krogh & Greve 2006).

4.2. Sampling design

The data used in this study is taken from the Danish National Forest Inventory and from the Danish SINKS project.

National Forest Inventory (NFI)

The Danish National Forest Inventory was initiated in 2002 and is now in its second cycle. The NFI includes about 5000 primary sampling units (PSU) located in a 2x2 km grid covering the whole of Denmark. About 1/3 of the PSUs are permanent and re-measured in five-year cycles. Each PSU consists of four circular secondary sampling units (SSU) with a radius of 15 m, located in the corners of a square of 200x200 m. If the SSU plot covers different land uses or tree species the plot is subdivided in tertiary sampling units (TSU). The sampling radius of 15 m in each SSU is subdivided in three circles, 3.5 m, 10 m and 15 m. Only plots where the forest cover had a minimum of 50% were selected. Following the analysis of aerial photos, the actual percentage of forest cover (X) has been calculated on each individual SSU (j):

$X_j = \frac{A_j}{A_{15,j}}$ where A is the forested area and A_{15} the total area of the 15m radius SSU (Nielsen et al. 2011).

The inventory follows the forest definition from the FAO (UNECE n.d.): "Land with tree crown cover […] of more than 10 % and area of more than 0.5 ha [and a minimum width of 20 m]. The trees should be able to reach a minimum height of 5 m at maturity in situ. […] firebreaks and other small open areas […]" that constitute an integral part of the forest, are also included.

SINKS project

The Danish SINKS project is an inventory of forest soil C under art. 3.4 of the Kyoto Protocol, aiming to reporting forest soil C dynamics. However, Denmark applies the "non-source" principle (see chapter 1.2) after providing sufficient information that Danish forest soils are not a source for C emissions (Sverrild et al. 2009). This principle enforces that Denmark does not have to report to the UNFCCC how much C is sequestered exactly in this pool but only needs to verify that this pool is not a source (Omogyi & Reudenschuss 2010).

To discover changes in soil C pools more efficiently, 277 plots that are located in the NFI project have been added to the SINKS project (Sverrild et al. 2009). For this study, only data from 2007 and onwards were available from the SINKS project.

4.3. Data acquisition of biomass and dead wood carbon

- The **biomass** C pool is defined as "Carbon in all living biomass above the soil, including stem, stump, branches, bark, seeds and foliage ", as well as "carbon in all biomass of live roots. Fine roots of less than 2 mm diameter are excluded, because these often cannot be distinguished empirically from soil organic matter or litter" (FRA 2010).
- **Dead wood** C encompasses "carbon in all non-living biomass not contained in the litter, either standing, lying on the ground, or in the soil. Dead wood includes wood lying on the surface, dead roots, and stumps larger than or equal to 10 cm in diameter […]"(FRA 2010).

The data for biomass C, including both (above-and belowground) biomass and dead wood, are derived from NFI plots. In order to compare the amount of C stored in biomass with the amount stored in forest floor and soil, only data from 2007 - 2011 was used from the NFI. Within the inner 5m circle of the SSU, a single caliper measurement of the diameter at breast height (DBH), of 1.3 m is taken of every tree. Trees with a diameter larger than 10 cm are measured in the 10 m circle. Within the 15 m circle, only trees with a diameter of more than 40 cm are included in the measurements. The same principles apply for measuring standing dead wood; as long as the DBH exceeds 4 cm. Lying dead wood is included within the whole plot when it has a diameter of more than 10 cm at the midpoint. For further measurements, about 2-6 trees are randomly selected. Total height, crown height, diameter at stump height and age are recorded. In addition, signs for the state of health, such as defoliation, discoloration, mosses and lichens are documented. The tree species composition as well as ground vegetation is registered for the whole plot and the forest floor layer is measured.

The collected data are used for further calculations e.g. the height of trees, the basal area per hectare of individual trees, the stem number per hectare, volume of each live tree as well as the volume of standing or lying dead wood and biomass of individual trees (Nielsen et al. 2011).

4.4. Data acquisition of soil and forest floor carbon

- The litter (**forest floor**) C pool comprises "carbon in all non-living biomass with a diameter less than the minimum diameter for dead wood [...], lying dead in various states of decomposition above the mineral or organic soil" (FRA) 2010).
- **Soil** C is defined as "organic carbon in mineral and organic soils (including peat) to a specified depth [...]"(FRA) 2010).

The basic data of this project were collected in 277 sampling plots of the National Forest Inventory. The plots were selected randomly among the permanent sampling plots of the NFI. The information, that is needed to estimate soil C and forest floor C, was derived from the SINKS project. These 277 plots are located at the same PSUs and SSUs as from the NFI plots. The sampling took place from 2007 to 2011.

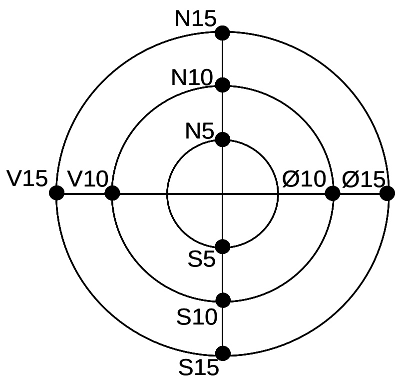


Fig. 6. Design of the Secondary Sampling Unit (SSU), with a radius of 15 m. The samplings of the forest floor and mineral soil are taken to the north, east, south and west, respectively with a radius of 5, 10 and 15 m from the middle point. They are displayed in the black dots, named N15, N10, N5 etc. In the middle of the SSU is a metal pin to help finding the plot.

In each SSU, 10 sampling points were identified (see the location of the sampling points in Fig. 6) (Sverrild et al. 2009). A frame of 25x25 cm was placed on each sampling point, the forest floor from this area was removed and the thickness of the forest floor was measured on all four sides. Soil cores were removed in the same 10 sampling points using an EJH auger soil corer of 2-2.5 cm in diameter, and each core was separated according to its depth: 0-10 cm, 10-25 cm, 25-50 cm, 50-75 cm and 75-100 cm soil depth. The samples of similar depths were pooled for all 10 sampling points, giving 5 soil samples in addition to the 10 forest floors samples (Sverrild et al. 2009).

4.5. Data acquisition of explaining variables

The following variables were considered to be of interest for explaining total C sequestered as well as C sequestered in the four pools (biomass, dead wood, forest floor and soil):

- soil category,
- tree species category as well as some specific tree species,
- stand age,
- crown cover,
- broadleaf fraction,
- tree species biodiversity,
- precipitation and
- previous land use.

The **soil category** has been defined according to the GEUS_25 soil map. As the GEUS_25 only has coverage of 85% of Denmark's land area, the GEUS_200 map has been used for missing data (Tab. 3).

Tab. 3. Definition and sample distribution of soil category on total sample plots.

Soil category	Definition	Frequency	%
Loamy	Soil types with the code: • DL ML (GEUS_25); Marine deposits of sand and clay (→“Marint sand og ler”), • Clayey till (→“Moræneler”), Glaciofluvial deposits of clay (→“Smeltevandsler”) (GEUS_200).	82	29.6
Organic	Soil types with the code: • FP FT (GEUS_25); • Freshwater sediments (→“Ferskvandsdannelser”) or Marsh (→"Marsk") (GEUS_200).	23	8.3
Sandy	Soil types with the code: • ES HS TG TS TS-TG YS S DG DS MG MS (GEUS_25); • Extra-marginal deposits (→”Extramarginale aflejringer"), Glaciofluvial deposits of sand and gravel (→"Smeltevandssand og -grus"), Sandy-gravelly till (→"Morænesand og grus"), Prequaternary (→"Prækvartær"), Older marine sediments (→"Ældre havaflejringer"), Drifting sand (→"Flyvesand") (GEUS_200).	172	62.1

For a more general perspective on the effect of different tree classes, a **tree species category** variable has been created. Based on the land use, it has been subdivided into (1) “Conifer forest” if they dominated more than 75% of the forested part of the sample plot, (2) “Broadleaf forest” if broadleaved trees cover more than 75% of the forested part of the sample plot, (3) “Mixed (conifer and broadleaf) forest” if broadleaved or coniferous trees have a dominance in between 25% and 75%. Finally, some plots that did not have a forest cover at the sampling time but still account as part of a forest or where the trees are smaller than 1.3 m and therefore no measurements could be taken, are regarded as (5) “Temporarily unstocked” (Tab. 4):

Tab. 4. Sample distribution of tree species category on total sample plots (n=277).

	Conifer forest	Broadleaf forest	Mixed	Temporarily unstocked
Frequency	114	110	47	6
%	41.2	39.7	17	2.2

With the purpose of examining the effect of the most common **single tree species** in Denmark on C sequestration potential nine species categories have been selected (Tab. 5). Precondition is that the fraction of the species belonging to the in Table 5 mentioned species categories is larger than 50%. This has been the case for only 185 out of 277 plots.

Tab. 5. Sample distribution of single tree species (n=185).

	Ash	Beech	Fir	Larch	Nordmann fir	Norway spruce	Oak	Pine	Sitka spruce
Frequency	7	41	12	11	10	32	23	28	21
%	2.5	14.8	4.3	3.9	3.6	11.6	8.3	10.1	7.6

Stand age, crown cover, broadleaf fraction and previous land use have been derived from the NFI data table, directly.

The **stand age** is defined as the average age of trees on SSU level. For plots that are subdivided in TSUs the stand age refers to the average age of trees from the biggest TSU. However, some plots were lacking data about the average age. In that case, either the age of the oldest tree was taken, if available, or the age of the same sampling plot from the first NFI (2002-2007) was used and the missing years were added. For instance, only the age of the plot from 2008 (second cycle of NFI) was missing but it was given for the same plot in the year 2003 (first cycle of NFI). Consequently, this age was added up by 5.

The **crown cover** is an estimate of the canopy cover on a percentage basis.

The species fraction of broadleaved trees calculates the **broadleaf fraction**. The species fraction is calculated as the fraction of the basal area on the forested part of the SSU.

The **previous land use (PLU)** is based on changes in land use since 1990. Either it is “forest remaining forest” (FRF), meaning that the area was forested before 1990 and still is, or it has been “afforested” (AFF) between 1990 and 2007.

The degree of tree species **biodiversity** for each plot is calculated by the Simpson Index, using the species fraction. It expresses the probability to not find the same species at two randomly selected spots within one plot.

The data for **precipitation** amount are calculated from samples taken in 10x10 km grid.

4.6. Laboratory preparation of soil and forest floor samples

Forest floor

The 10 samples of the forest floor of each SSU plot were dried at 40°C until the largest forest floor samples did not lose weight, or did lose less than 1 g, from one day to the next, thus, a constant weight was reached. The samples were weighed 30 min after they have been removed from the drying oven. Then, the mineral soil particles, green plant material and large roots were removed before weighing a last time. Subsequently, they were ground in a Retsch SM 2000 mill through a 2 mm sieve. In addition, 10% of each of the 10 samples was mixed to a composite sample out of which a subsample of 100 ml was taken for further finer grinding with a Tecator mill.

Soil

The merged samples from each of the 5 soil layers for each SSU plot were dried at 40°C until a constant weight was detected. While sandy soil samples could be sieved or crushed directly, more clay-rich soils were ground in a mortar until it could be sieved to 2 mm. Stones, bigger than 2 mm, were extracted and weighed separately. Before weighing the fine soil was dried again at 40°C for a minimum of 48 hours. Thereafter, a subsample of 20 g was taken for finer grinding in an agate mortar.

4.7. Chemical analysis

All samples were sent to Agrolab/Institut Koldingen, Sarstedt, Germany, for chemical analysis. A dry combustion method (Elementar analyzer, ISO 10694) was used to determine total organic C in the forest floor and in the soil samples. Carbonates were removed prior to the analysis.

4.8. Calculations of carbon stocks

Calculation of biomass carbon

Calculating biomass C of above- and belowground biomass begins with estimating species specific volume (based on Madsen 1987 and Madsen & Heusèrr 1993) and expansion factor. For the latter purpose the species were only subdivided in conifers and deciduous for which an expansion factor model developed for Norway spruce (=1.8) and beech (=1.2), respectively, was applied. After that, the biomass (B) of each tree (i) per sample plot (j) as the total volume (V_{Tot}) multiplied with the density specific for the respective specie (based on Moltesen, 1988 in Nielsen et al. 2011).

$$B_{ij} = V_{Tot} \cdot \mathrm{Density}_{ij}$$

A C percentage of 50% for biomass was assumed. Following, the biomass of each tree, C (C) of each tree (i) on each plot (j) can be calculated as:

$$C_{ij} = B_{ij} \cdot 0.5$$

To estimate the total biomass C stock (C, t ha-1) for each plot, the biomass C stock in every circle (3.5m, 10m, 15m) in each plot at TSU level, was calculated before the average area weighted C of each circle could be estimated. Until, finally, the overall average C per hectare for each sample plot is multiplied with the forest area.

$$C = (C_{3.5} + C_{10} + C_{15}) \cdot A_{Skov}$$

Calculation of dead wood carbon

The calculation of standing dead wood C is similar to biomass C. First of all, the same volume functions and expansion factor as for estimating biomass C was used. Then, the biomass (B_s for standing and B_l for lying dead wood) of each tree (i) in each sampling plot (j) was calculated. Besides the volume (V_s, V_l) and species specific density, a reduction factor (r_k) giving the structural decay of the wood was added.

$$B_{s,ij} = V_s \cdot Density_{ij} \cdot r_{k,\,ij}$$

$$B_{l,ij} = V_l \cdot Density_{ij} \cdot r_{k,\,ij}$$

Again, a C percentage of 50% for dead wood biomass was assumed. Thus, the biomass of each tree and the C (K) of each tree (i) of each plot (j) can be calculated as:

$$K_{s,ij} = B_{s,ij} \cdot 0.5$$

$$K_{l,ij} = B_{l,ij} \cdot 0.5$$

To estimate the total dead wood C stock (K_D, t ha^{-1}) for each plot, the dead wood C stock in every circle (3.5m, 10m, 15m) in each plot at TSU level, including both standing and lying dead wood, was calculated before the average area weighted dead wood C of each circle could be estimated. For the last step, the overall average C per hectare for each sample plot is multiplied with the forest area.

$$K_D = (C_{3.5} + C_{10} + C_{15}) \cdot A_{Skov}$$

For final analysis, the biomass and dead wood data of TSU level are weighted for SSU level.

Calculation of forest floor carbon

The forest floor C stock (t ha^{-1}) was calculated by the dry weight $DW_{ff2007\text{-}2011}$,i of each individual forest floor sample number i (i=1-10) in g and the C concentration $c_{ff2007\text{-}2011}$ of the pooled sample in mg g^{-1}:

$$C_{ff2007\text{-}2011} = \sum_{i=1}^{10} DW_{ff2007\text{-}2011,\,i} \cdot 0.0016 \cdot c_{ff\,2007\text{-}2011}$$

Calculation of soil carbon

The mineral soil C stock (t ha^{-1}) was calculated by the depth d_m of the given horizon (m) in cm, the relative volume of the stone content $RV_{stone2007\text{-}2011}$ (>2mm) without unit, the bulk density of soils ρ_{soil} in g cm^{-3} (fine soil < 2mm) and the C concentration $c_{soil2007\text{-}2011}$ in mg g^{-1}:

$$C_{\mathrm{m}2007\text{-}2011} = \sum_{i=1}^{4\,(or\,5)} d_{\mathrm{m}\text{-}2011} \cdot 10000 \cdot (1 - RV_{\mathrm{stone}\,2007\text{-}2011}) \cdot \rho_{\mathrm{soil}} \cdot c_{\mathrm{soil}\,2007\text{-}2011}$$

(Nielsen et al. 2011)

The soil bulk density was estimated using the pedotransfer functions by Vejre et al. (2003).

4.9. Statistical analysis

Once the dataset was finalized and the explanatory variables defined, the same statistical analysis was applied for all dependent variables (total forest C stock and all C pools). The final data set was still missing some data. Precipitation and biomass data were missing for 2 and 10 plots out of 277, respectively. Since 6 plots were defined as temporarily unstocked, the broadleaf fraction is regarded as missing for those plots. Moreover, the broadleaf fraction is missing for 2 more plots because the species fraction has not been given, for the same reason, the same 8 plots plus one for the biodiversity index is also missing. Originally, information on biomass C was missing for 16 plots. For 6 out of these, data were also missing for crown cover, tree species and stand age. According to their land use and after comparing aerial pictures on GIS, these 6 plots were defined as temporarily unstocked. As a consequence, the missing variables were attributed the value zero.

All effects were analysed using a general linear model (GLM). This has been done for each dependent variable separately by the proc GLM procedure in SAS 9.2 (SAS Institute Inc. n.d.) using the method of least squares. The least square mean (LSMean) was chosen in order to compare the different average C content of the unbalanced categorical variables. It estimates the marginal or within-group mean considering the different size of the compared groups (unbalanced data). The LSMean is based on the model used (SAS Institute Inc. 2009).

Due to the large number of explanatory variables, the GLM select statement was applied to detect the order of those variables and its second order interactions that result in the best model fit. To determine statistical significance for entry and removal to the selection process the significance level α was set to 0.05. The null hypothesis was defined as the explanatory variables not having significant influence on the response variable.

After the order of the variables has been determined with the GLM select statement, the pure GLM procedure was applied in order to get the final parameter estimates and p-values. Within the GLM procedure multiple regression analysis and one-way ANOVA was conducted to find possible relationships between response and explanatory variables that have a significant effect on C storage. Furthermore, the Tukey-Kramer procedure was used to detect significant differences among the categorical variables' means and adjust for their homogeneity of variance (SAS Institute Inc. 2009).

Finally, a best model fit was taken to gain parameter estimates with which it should be possible to predict total C content and C content of each pool, respectively. The model-output derived from GLM was further examined on a graphical basis. This led to an occasional exclusion of one variable because the choice made by the GLM select process of having a significant effect on C storage was based on <10 plots and hence not statistically sound (Tab. 6 and Tab. 7). The p-values in the model were taken from the Type III sum of squares.

Tab. 6. Sample distribution (frequency) of tree species category on soil category and previous land use.

		Conifer	Broadleaf	Mixed	Temporarily unstocked
	Loamy	17	55	10	0
	Organic	2	18	3	0
	Sandy	95	37	34	6
	Stand age	33	58	43	0
PLU	*AFF*	3	4	3	0
	FRF	111	106	44	6

Tab. 7. Sample distribution (frequency) of single tree species on soil category and previous land use.

		Ash	Beech	Fir	Larch	Nordmann fir	Norway spruce	Oak	Pine	Sitka spruce
	Loamy	3	28	3	2	4	8	7	1	2
	Organic	2	3	0	1	0	0	1	0	1
	Sandy	2	10	9	8	6	24	15	27	18
	Stand age	46	73	34	38	21	35	48	35	31
PLU	*AFF*	0	1	0	0	0	3	1	0	0
	FRF	7	40	12	11	10	29	22	28	21

When (as it was the case for total, dead wood and soil C) the effect of broadleaf fraction was found to be significant by the GLM select procedure, the graphical analysis revealed that this effect was only due to some plots with 100% broadleaf fraction having a larger C stock than plots with less than 100% broadleaf fraction. This suspicion was confirmed by running the model with the modified broadleaf fraction (plots that have 0 and 100% broadleaf cover have been removed) resulting in the non-significance of the broadleaf fraction. Instead, the tree species category entered the model. For the forest floor C model the broadleaf fraction was still significant, but while excluding this variable, the tree species category appeared significant. Moreover, this model yields a higher coefficient of determination (r^2). In addition, it was checked that the interactions involving tree species category never based solely on temporarily unstocked areas. The parameter estimates for the final model are given in Tab. 9, Tab. 11, Tab. 13, Tab. 14, Tab. 16, Tab. 18, Tab. 20, Tab. 21 and Tab. 23.

In order to fulfil the statistical requirement of normal distribution of the residuals, all but one of the dependent variables were $\log_e$-transformed; for biomass data, the square root was taken. The normality was tested with the Anderson-Darling test and verified by the plot of quantiles using the Univariate procedure in SAS Stat Version 9.2 (SAS Institute Inc. n.d. a). The total following analysis was conducted on the transformed variables. For presentational purposes of the results the variables were back-transformed.

A basic statistical summary, including the number of observations, the mean (for comparing the C pools) and LSmean (for comparing the categorical variables within the models for each C pool), the standard error of the mean (Std. Err.), the 95% confidence interval limits as well as the minimum and maximum value, was produced for total forest C, biomass, dead wood, forest floor and soil C stock (Tab. 8) as well as for the categorical variables based on the respective model

(Tab. 10, Tab. 12, Tab. 15, Tab. 17, Tab. 19, Tab. 22, Tab. 24). In addition, the frequency distribution was created for tree species category and single tree species on soil category, stand age and previous land use respectively (Tab. 6 and Tab. 7).

5. Results

The focus is on those variables that appear to have a significant effect on the C sequestration potential for each pool respectively as well as for the total forest C content per hectare.

As expected, the largest C stock of our sampling plots is in forest soils. It accounts for about 66.5% of total C stored in Danish forests. Biomass (above- and belowground) constitutes the second highest stock with 27.4%, whereas only small amounts are stored in forest floor (6.6%) and dead wood (0.4%) (Fig. 7). When comparing the mean biomass C stock with the other C pools, it has to be considered that the number of plots for biomass C stock is 10 less than for the other pools. Thus, the relative biomass C stock could be slightly over- or underestimated. More detailed numbers about the mean, standard error of the mean, 95% confidence interval and minimum and maximum amounts, are shown in table 8.

Tab. 8. Basic statistics of total carbon stock and the four carbon pools.

CARBON STOCK (t/ha^{-1})	Number of plots	Mean	Std. Err.	95% confidence limits		min.	max.
				lower	upper		
Total	277	279	8.54	262	296	78.4	942
Biomass	267	81.2	4.27	72.8	89.6	0	440
Dead wood	277	1.16	0.19	0.79	1.53	0	22.7
Forest floor	277	15.3	0.89	13.6	17.1	0.24	69.5
Soil	277	184	7.33	170	199	36.6	698

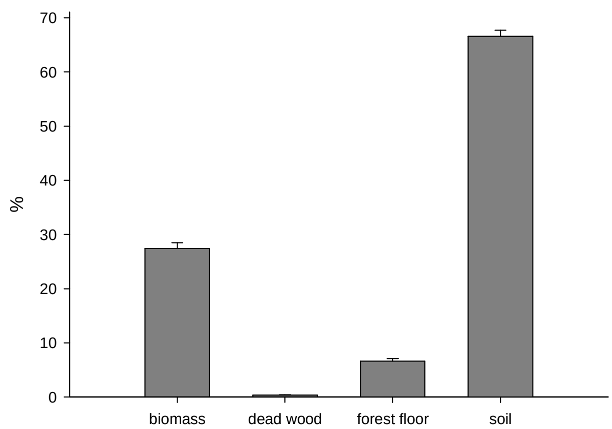


Fig. 7. Average relative carbon content of each pool.

5.1. Total carbon stock

For total C stock, the best fitted model explained 47% of the variance (Tab. 9). Stand age was the single factor which explained the largest part of the variance. It amounts almost 20%. Additional 15% of the variance can be attributed to the soil category. On average, organic soils store the most C (Appendix V), and the C stock in organic soils is significantly different from the C stock of other soil categories. However, the total C stock on organic soils decreases with increasing stand age, whereas the C content in loamy and sandy soils increases with stand age (Fig. 8, left). The decreasing trend for C in organic soils is due to only two observations in older stands. This makes the interaction between soil category and stand age uncertain. Furthermore, the amount of variance explained for all three significant interactions is very small, probably uncertain, and therefore not further interpreted.

Tab. 9. Model results for total carbon stock: significant effects influencing total carbon stock, $\log_e$-transformed (n=277).

Final Model: $\log_e$ Total C	I	A	B	C	C*A	D	C*D	A*B
	intercept	**stand age**	**soil category**	**crown cover**	**crown cover * stand age**	**tree species category**	**crown cover * tree species category**	**stand age * soil category**
p-value	<.0001	0.005	<.0001	<.0001	0.04	0.0001	0.002	0.01
r^2		0.17	0.35	0.38	0.39	0.43	0.45	0.47
parameter estimate	4.91	0.01	Loamy 0.03 Organic 0.97 Sandy 0	0.01	-0.00008	Broadleaf 0.18 Conifer -0.55 Mixed -0.49 temp.unst. 0	*Broadleaf -0.008 *Conifer -0.0009 *Mixed 0 *temp.unst. 0	*Loamy -0.0006 *Organic -0.008 *Sandy 0

$$\text{Total Carbon} = I + a \cdot A + B + c \cdot C + (a+c) \cdot A^*C + D + c \cdot C^*D + a \cdot A^*B$$

a, c = observed values for stand age and crown cover respectively

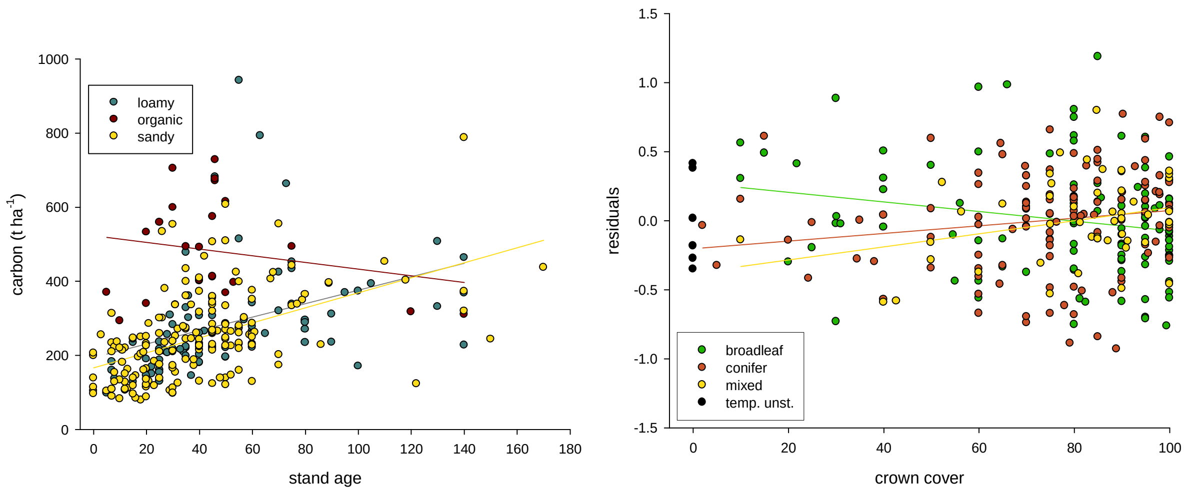


Fig. 8. Total C stock as a function of stand age for different soil category (**left).** Influence of crown cover and tree species category on total carbon stock after the effects of the variables before (1. effect: stand age. 2. effect: soil category. 3. effect: crown cover. 4. Effect: tree species category) have been removed. Shows how much is explained by the added variable on the X-axis (**right**).

In comparison to conifer and mixed forests, broadleaf forests store significantly more C (317 t ha^{-1}). Conifer trees have the lowest C content (262 t ha^{-1}), while mixed broadleaf and conifer forests have the highest variation in C contents (Tab. 10). None of the differences between single tree species were significant, even though it amounts to almost 100 t C ha^{-1} (in case of ash and pine). Nevertheless, the single tree species representing broadleaf forests store on average more C (~283 t C ha^{-1}) than conifer species (~269 t C ha^{-1}); albeit all conifers but pine have a higher C content than oak forests (Tab. 10).

The C content stored in broadleaf forests is decreasing with increasing crown cover. However, in order to examine the effect of the interaction of tree species category and crown cover, a sequence of residual plots were made (see Appendix V). Now, it becomes obvious that regarding the interaction of tree species category and crown cover, broadleaf as well as conifer forests still have an increasing effect on C storage while having a bigger crown cover, even though it is not a strong one (Fig. 8, right). Yet, mixed forests show the highest increase in C stock with expanding crown cover.

Tab. 10. Basic statistics of total carbon stocks distributed to soil category, tree species category and single tree species.

TOTAL C (t ha^{-1})	**LSMean**	**95% confidence limit**	
		lower	**upper**
Loamy	Non-est. ^{a}		
Organic	Non-est. ^{b}		
Sandy	Non.est. ^{a}		
Conifer	262 ^{a}	237	287
Broadleaf	317 ^{b}	293	340
Mixed	299 ^{ab}	265	337
Temp. unst.	Non-est.		

Note: $^{a\ b}$ indicate significant differences within one group; | temp. unst. means temporarily unstocked; | non-est. means not estimable. | In order to get the LSMean for the tree species category, the tree species category variable was replaced by the single tree species variable, using the same model.

5.2. Individual carbon pools

5.2.1. Biomass

The model for biomass C stock has the highest determination coefficient (r^2=0.53) of all (Tab. 11). The variation in C content in biomass is mainly explained by stand age and crown cover, with the amount of variance explained with only stand age and crown cover included, reaching 39% and 14%, respectively. In addition, the effect of soil category is explaining an additional 2% of the variance. Carbon storage in biomass does not increase linearly with stand age but tends to stabilise when the trees are more than 100 years old (Fig. 9, left). At the first glance, increasing crown cover is accompanied with an increasing biomass C stock (Fig. 9, right). However, per definition a high crown cover does not automatically include a high biomass C stock. It only shows the percentage of the covered area, meaning that a high crown cover can consist of many young trees (with a lower biomass C stock each) on the one hand and of older trees that store on average more C than younger ones, on the other hand.

Tab. 11. Model results for biomass carbon stock: significant effects influencing biomass carbon stock, square-root transformed (n=267).

	I	A	B	C
FINAL MODEL: SQRT BIOMASS C	**intercept**	**stand age**	**crown cover**	**soil category**
p-value	0.33	0.05	<.0001	<.0001
r^2		0.39	0.52	0.53
parameter estimate	0.12	0.06	0.06	Loamy 1.09 Organic 0.32 Sandy 0

$$\text{Biomass Carbon} = I + a \cdot A + b \cdot B + C$$

a, b = observed values for stand age and crown cover respectively

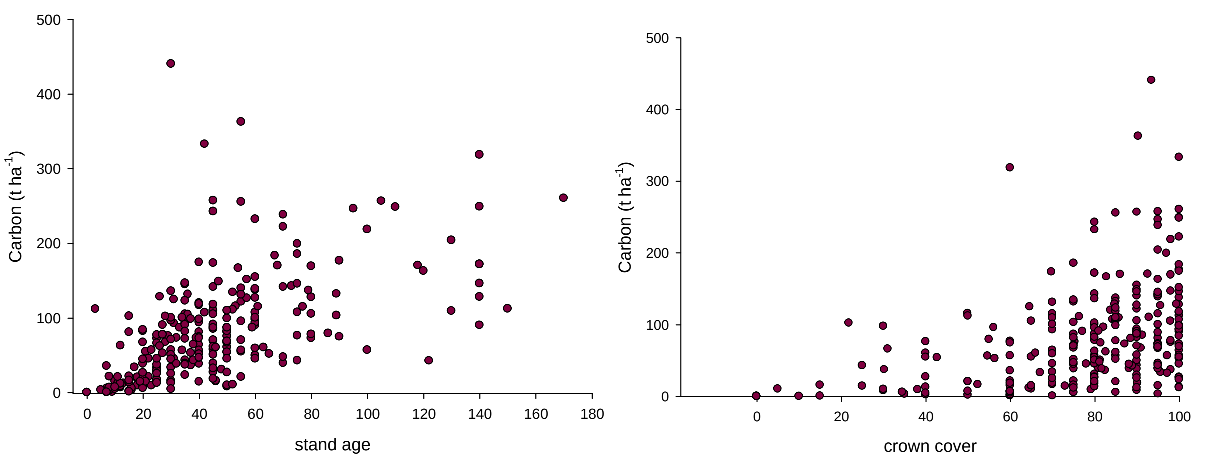


Fig. 9. Biomass carbon by stand age (**left**) and by crown cover (**right**).

Unlike the effect of the different soil categories on total C, the biomass C pool is significantly larger in areas with loamy soils (on average 78 t ha^{-1}), followed by sites with organic soils (on average 65 t ha^{-1}), with the generally lowest amount of C in biomass found on the sandy soils (on average 60 t ha^{-1}) (Tab. 12).

Tab. 12. Basic statistics of biomass carbon stocks distributed to soil category.

BIOMASS C (t ha^{-1})	LSMean	95% confidence limits	
		lower	upper
Loamy	78.4 [a]	68.1	89.4
Organic	65.4 [a]	48.3	85.0
Sandy	60.2 [b]	53.9	66.9

5.2.2. Dead wood

The model for dead wood C pool is the least fitting (r^2=0.04). Only crown cover showed a significant effect (see Appendix IV). According to the parameter estimate increasing crown cover causes a decrease in dead wood C. Looking at Fig. 10, however, the opposite seems to be true.

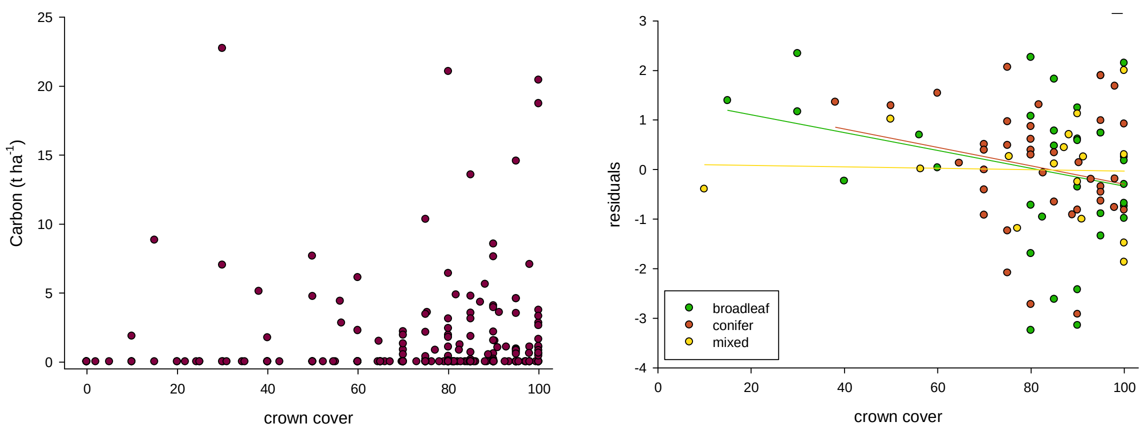


Fig. 10. Dead wood carbon by crown cover (**left**). Influence of the interaction of crown cover and tree species category on dead wood carbon stock after the effect of the variable before (crown cover) has been removed. Shows how much is explained by this interaction (**right**).

The tree species category does not have a significant effect. However, the interaction of crown cover and tree species category is almost significant (p-value = 0.0575) (Tab. 13). This model explains almost three times as much variation (r^2=0.11) as the one with crown cover as the single effect. It becomes obvious that the interaction of crown cover with broadleaves and conifers results in a decreasing adjustment of the curve (Fig. 10, right), while mixed forests seem to have a higher dead wood C content (Tab. 13).

Tab. 13. Model results for dead wood carbon stock: significant effects influencing dead wood carbon stock, log_e-transformed (n=87).

	I	A	B
FINAL MODEL: LOGe DEAD WOOD C	**intercept**	**crown cover**	**crown cover*tree species category**
p-value	1.92	0.03	0.06
r^2		0.05	0.11
parameter estimate		-0.01	*Broadleaf -0.004 *Conifer -0.01 *Mixed 0

Dead Wood Carbon= I+a·A+a·B

a = observed value for crown cover

5.2.3. Forest floor

The best fitted model for the forest floor C pool explains 38% of the variation. Six variables had a significant effect on forest floor C stock (Tab. 14). About 29%, which is more than 75% of what the total model to predict forest floor C explains, is explained by tree species category and stand age. The effect of precipitation, the interaction of stand age and tree species category describe the remaining variance; about 5% and 3% each. Finally, previous land use contributes to 2% of the explained variance.

Tab. 14. Model results for forest floor carbon stock: significant effects influencing forest floor carbon stock, log_e-transformed (n=275).

	I	A	B	C	B*A	D
FINAL MODEL: LOGe FOREST FLOOR C	**intercept**	**tree species category**	**stand age**	**precipitation**	**stand age * tree species category**	**previous land use**
p-value	0.03	0.005	<.0001	<.0001	0.0005	0.01
r^2		0.22	0.29	0.34	0.37	0.39
parameter estimate	-1.87	Broadleaf 1.23 Conifer 1.40 Mixed 1.50 Temp.unst. 0	0.02	0.003	*Broadleaf -0.01 *Conifer 0.008 *Mixed 0 *Temp.unst. 0	AFF -0.75 FRF 0

Forest Floor Carbon= I+A+b·B+c·C+b·B*A+D

b, c = observed values for stand age and precipitation respectively

In forest floors of conifer forests the C stock is up to 2.5 times higher than in broadleaf forests (Tab. 15). The lowest C stock in forest floors of mixed forests is still higher than the highest values found for broadleaf forests. This is also reflected by the single tree species. Only fir and Nordmann fir do not differ significantly from broadleaf species. For all but one plot each for conifer and mixed forests, only broadleaf forests reach a higher age than 100 years (Fig. 11, top). As a conclusion, the older stands have a higher forest floor C stock than younger ones. However, five plots with beech and three plots with oak contain much more forest floor C than the other broadleaf species (Fig. 11, bottom left). Except one plot with beech which is located on loamy soils, they are all situated on sandy soils.

Tab. 15. Basic statistics of forest floor carbon stocks distributed to PLU, tree species category and single tree species.

Forest Floor C (t ha^{-1})		LSMean	95% confidence limits lower	upper
PLU	***AFF***	Non-est.		
	FRF	Non-est.		
Conifer		11.5 [b]	8.12	16.2
Broadleaf		4.14 [a]	3.01	5.69
Mixed		8.78 [b]	6.12	12.6
Temp. unst.		Non-est.		
Ash		2.62 [a]	1.32	5.19
Beech		5.89 [a]	3.99	8.68
Fir		7.75 [ab]	4.29	14
Larch		16.6 [b]	9.39	29.2
Nordmann fir		9.82 [ab]	9.19	21.0
Norway spruce		13.9 [b]	9.19	21.0
Oak		5.08 [a]	3.35	7.69
Pine		20.2 [b]	13.1	31.3
Sitka spruce		17.9 [b]	10.4	30.6

Note: [a] [b] indicate significant differences within one group; | temp.unst. means temporarily unstocked; | non-est. means not estimable. | In order to get the LSMean for the tree species category, the tree species category variable was replaced by the single tree species variable, using the same model.

In comparison to the other pools, the forest floor model is the only one where previous land use has a significant effect. The C content is significantly lower on afforested areas than on those areas that have been covered by forests also before 1990 (Appendix V).

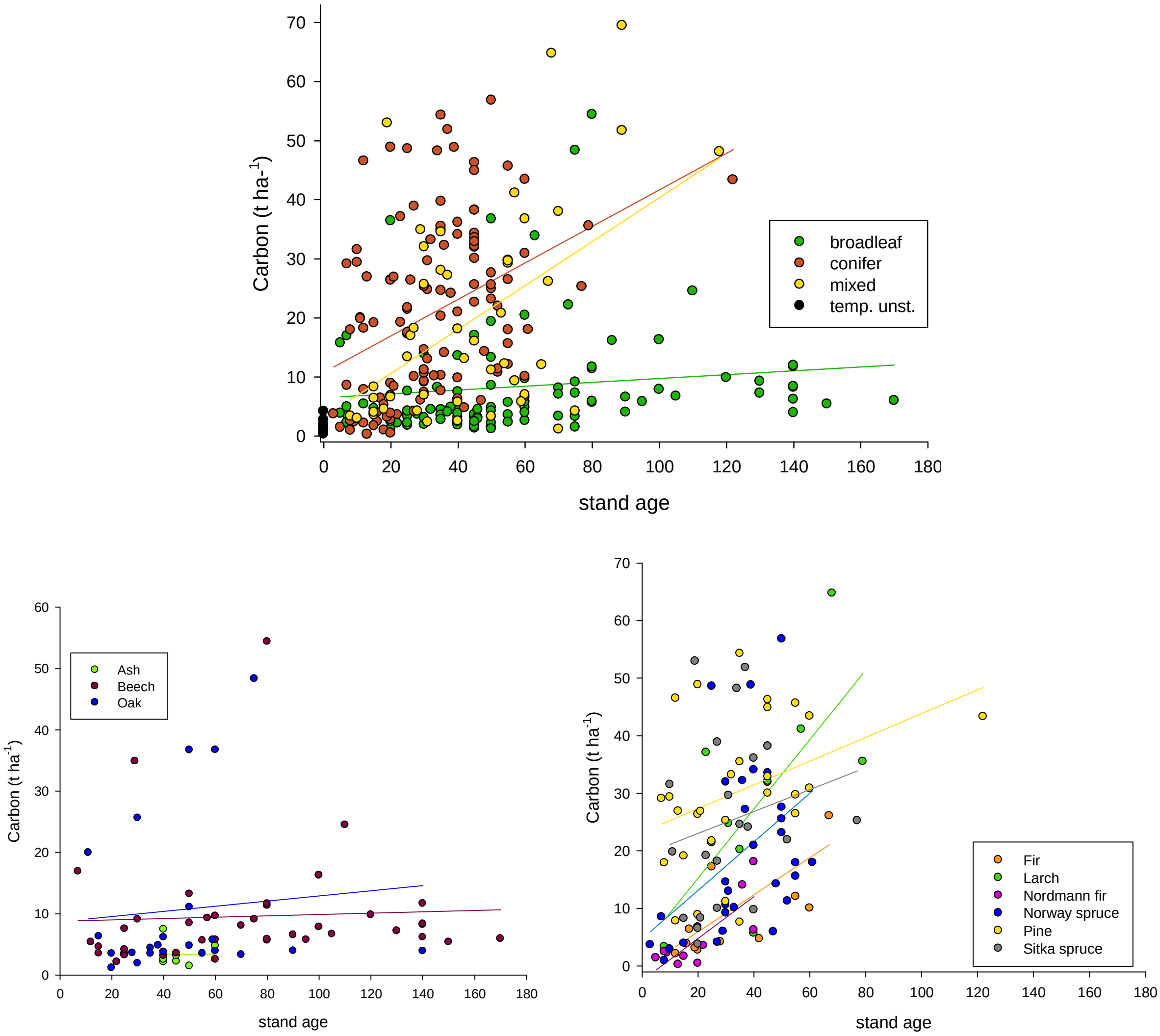


Fig. 11. Forest floor carbon stock as a function of stand age for different tree species categories (**top**). Forest floor carbon stock as a function of stand age by single tree species (**bottom left**: broadleaf species; **bottom right**: conifer species).

5.2.4. Soil

The final model for soil C reaches a coefficient of determination (r^2), of 0.30. Most of the factors influencing the C stock are explained by the soil category (~22%). In addition to soil category, it appears significant whether it is a broadleaf, conifer or mixed forest (Tab. 16). Organic soil differs significantly from the others (Tab. 17). It stores about twice as much C as loamy or sandy soils. Even the lowest value in the 95% confidence interval is 46% higher than the highest value in the interval of loamy and sandy soils. Soils under conifer forests store least C – about 31% less than broadleaf forests, which is even less than under temporarily unstocked areas. However, conifer and temporarily unstocked areas show no significant difference. The difference between conifer and broadleaf forests is confirmed by single tree species. Soils under ash, beech and oak have the highest C content. There is a significant difference between pine and all broadleaf tree species as well as between pine and Norway spruce.

Tab. 16. Model results for soil carbon stock: significant effect influencing soil carbon stock; $\log_e$ -transformed (n=277).

	I	A	B
FINAL MODEL: $\log_e$ SOIL C	**intercept**	**soil category**	**tree species category**
p-value	<.0001	<.0001	<.0001
r^2		0.22	0.30
parameter estimate	4.90	Loamy -0.04	Broadleaf 0.29
		Organic 0.72	Conifer -0.08
		Sandy 0	Mixed 0.20
			Temp.unst. 0

Soil Carbon= I+A+B

Tab. 17. Basic statistics of soil carbon stocks distributed to soil category, tree species category and single tree species.

SOIL C (t ha⁻¹)	LSMean	95% confidence limits lower	upper
Loamy	143 [a]	124	164
Organic	306 [b]	248	378
Sandy	149 [a]	134	165
Conifer	156 [a]	139	174
Broadleaf	225 [b]	205	246
Mixed	206 [b]	179	238
Temp. unst.	168 [ab]	117	243
Ash	243 [a]	178	330
Beech	169 [a]	147	194
Fir	161 [ab]	126	205
Larch	146 [ab]	113	187
Nordmann fir	166 [ab]	128	217
Norway spruce	168 [a]	143	1967
Oak	177 [a]	148	212
Pine	115 [b]	96.2	137
Sitka spruce	164 [ab]	135	199

Note: [a b] indicate significant differences within one group; | temp.unst. means temporarily unstocked. | In order to get the LSMean for the tree species category, the tree species category variable was replaced by the single tree species variable, using the same model.

5.3. Relative carbon stock

The statistical analysis for the relative C stock results in the discovery of those effects that are of significant importance for the respective C pool when all four pools have an equal share on the total C stock. The models contain those variables that are of significant importance for each C pool relative to the total C stock that is the sum of all four pools. Thus, the model for the relative C stock shows only those variables that have a pure effect on the respective pool and gives the C stock in the categorical variables as a percentage basis.

5.2.5. Biomass

The best fitted model for the relative biomass C stock explains 53% of the variance (Tab.18) and is very similar to the absolute model (Tab. 11). The main proportion of the variance is explained by stand age and crown cover, while the impact of soil category and tree species category is rather minor. As for the absolute biomass C stock, the relative biomass C stock shows the same increase with stand age and crown cover (Fig. 12) and forests on loamy and sandy soils have the biggest share on the relative biomass C stock. In contrast to the absolute stock where forests on loamy and organic soils have a significantly different biomass C stock from sandy soils, the relative biomass C stock shows a significant difference between stands on loamy soils from stands on organic and sandy soils (Tab. 19).

Tab. 18. Model results for relative biomass carbon stock: significant effects influencing relative biomass carbon stock; sqrt-transformed (n=267).

	I	A	B	C	D
FINAL MODEL: SQRT RELATIVE BIOMASS C	**intercept**	**stand age**	**crown cover**	**soil category**	**tree species category**
p-value	0.01	<.0001	<.0001	<.0001	0.01
r^2		0.30	0.49	0.53	0.53
parameter estimate	0	0.03	0.03	Loamy 0.80	Broadleaf 0.61
				Organic -0.67	Conifer 1.21
				Sandy 0	Mixed 1.07
					Temp. unst. 0

Relative Biomass Carbon= I+a·A+b·B+C+D

a, b = observed values for stand age and crown cover respectively

Regarding the tree species category, conifer-dominated forests contain significantly more C, compared to broadleaf stands (Tab. 19). The C stock of mixed forests shows a higher variation than the one of conifer forests and its mean is just slightly lower. For temporarily unstocked forests, the high variability results from the varying crown cover of those stands.

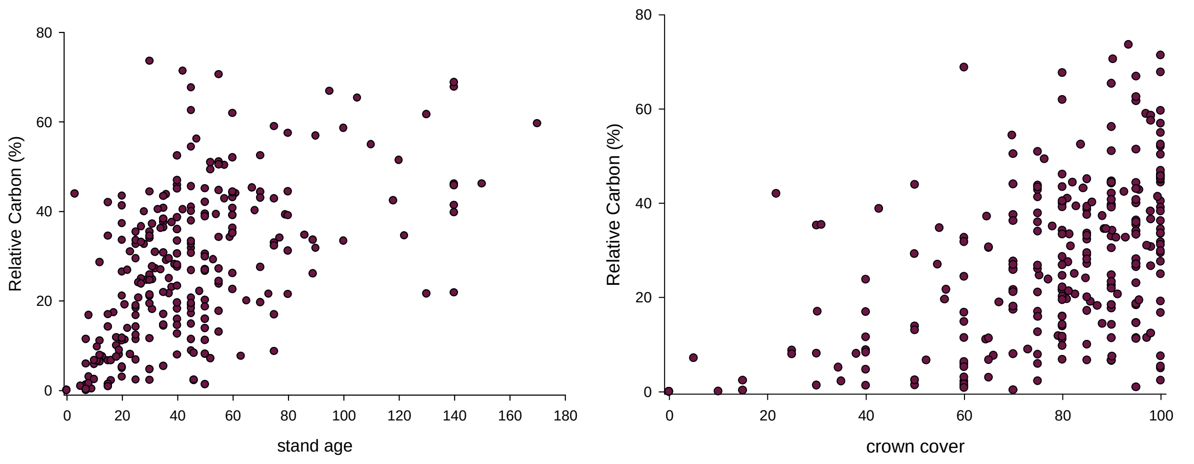


Fig. 12. Relative biomass carbon by stand age (**left**) and by crown cover (**right**).

Tab. 19. Basic statistics of relative biomass carbon stocks distributed to soil category and tree species category.

Relative Biomass C (%)	LSMean	95% confidence limits lower	95% confidence limits upper
Loamy	28.0 [a]	23.5	32.8
Organic	14.9 [b]	9.96	20.1
Sandy	20.2 [b]	17.2	23.3
Conifer	25.2 [ac]	21.8	28.8
Broadleaf	19.5 [b]	17.1	22.1
Mixed	23.8 [bc]	19.8	28.2
Temp. unst.	14.5 [bc]	6.49	25.7

Note: [a b c] indicate significant differences within one group.

5.2.6. Dead wood

The model for relative dead wood C stock is the least fittable, reaching a coefficient of determination of only 0.05 (Tab. 20). Crown cover is the only effect likely to influence this relative C pool. However, the graphical analysis (Fig. 13) supports the assumption that crown cover is rather an occasional effect chosen to significantly influence the relative dead wood C stock.

Tab. 20. Model results for relative dead wood carbon stock: significant effects influencing relative dead wood carbon stock; $\log_e$ –transformed (n=87).

FINAL MODEL: $\log_e$ RELATIVE DEAD WOOD C	I **intercept**	A **crown cover**
p-value	0.1469	0.0242
$\mathbf{r^2}$		0.06
parameter estimate	0.83	-0.02

Relative Dead Wood Carbon= I+A

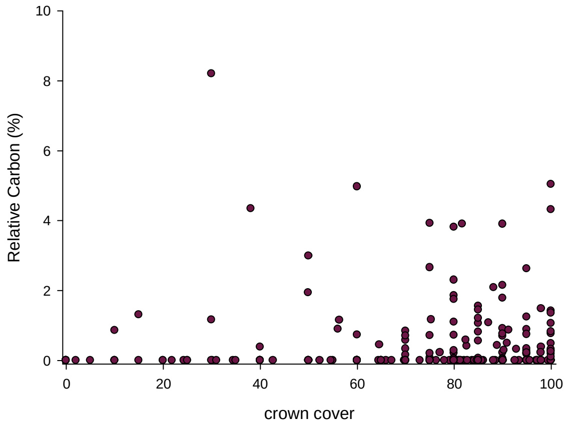


Fig. 13. Relative dead wood carbon by crown cover.

5.2.7. Forest floor

The final model for estimating the relative forest floor C stock accounts for 41% of the total effects influencing the C stock. Tree species category describes more than half of it. Precipitation, stand age, PLU and the interaction of stand age and tree species category only play a secondary role, raising the determination coefficient together by an additional 11% (Tab. 21).

Conifer dominated stands contribute a significantly greater share on the relative forest floor stock than broadleaf forests (Tab. 22). The same is true for mixed stands which also differ significantly from broadleaf dominated forests. Moreover, with an increasing stand age, the relative forest floor C stock rises as well (Fig. 14). Additionally, PLU displays a significant difference in forest floor C stock. Forests that have been remaining as forests since 1990 show a higher relative forest floor C stock than those that have been afforested (see Appendix VI).

Tab. 21. Model results for relative forest floor carbon stock: significant effects influencing relative forest floor carbon stock; $\log_e$ –transformed (n=275).

	I	A	B	C	D	C*A
FINAL MODEL: LOGe RELATIVE FOREST FLOOR C	**intercept**	**tree species category**	**precipitation**	**stand age**	**plu**	**stand age*tree species category**
p-value	0.0002	0.003	<.0001	0.0003	0.01	0.03
r²		0.31	0.36	0.38	0.40	0.41
parameter estimate	-2.50	Broadleaf 0.63	0.003	0.009	AFF -0.76	*Broadleaf -0.005
		Conifer 1.29			FRF 0	*Conifer 0.008
		Mixed 1.21				*Mixed 0
		Temp.unst. 0				*Temp. unst. 0

Relative Forest Floor Carbon= I+A+b·B+c·C+D+c·A*D

b, c = observed values for precipitation and stand age respectively

Tab. 22. Basic statistics of relative forest floor carbon stocks distributed to PLU and tree species category.

RELATIVE FOREST FLOOR C (%)		LSMean	95% confidence limits lower	upper
PLU	***AFF***	Non-est.		
	FRF	Non-est.		
	Conifer	5.00 b	3.53	7.09
	Broadleaf	1.43 a	1.03	1.97
	Mixed	3.25 c	2.26	4.68
	Temp. unst.	Non-est.		

Note: a b c indicate significant differences within one group.

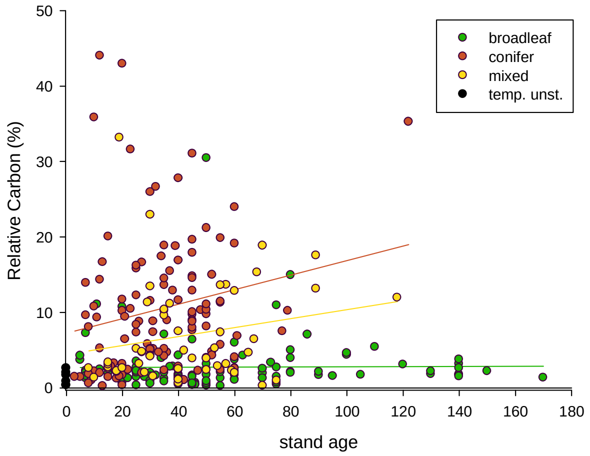


Fig. 14. Relative forest floor carbon stock as a function of stand age for different tree species categories.

5.2.8. Soil

In total, the r^2 amounts to 0.42 (Tab. 23). Stand age and crown cover constitute the largest effect (r^2=0.35 together) on the relative soil C stock. While stand age and crown cover are increasing, they both show a decline in the relative soil C stock (Fig. 15, top left). Broadleaf fraction, soil category and the interaction of stand age and tree species biodiversity account for the remaining 7%. A conifer fraction of 100%, which is equivalent to a broadleaf fraction of 0, indicates a positive adjustment of the curve of the relative soil C stock than a broadleaf fraction of 100% (Fig. 15, top right).

Tab. 23. Model results for relative soil carbon: significant effects influencing relative soil carbon stock; sqrt – transformed (n=268).

	I	A	B	C	D	A*E
FINAL MODEL: SQRT RELATIVE SOIL C	**intercept**	**stand age**	**crown cover**	**broadleaf fraction**	**soil category**	**stand age*biodiversity**
p-value	<.0001	<.0001	<.0001	<.0001	0.004	0.02
r^2		0.26	0.35	0.39	0.42	0.43
parameter estimate	9.68	-0.02	-0.01	0.70	Loamy -0.20 Organic 0.50 Sandy 0	0.003

$$\text{Relative Soil Carbon} = I + a \cdot A + b \cdot B + c \cdot C + D + (a+e) \cdot A*E$$

a, b, c, e = observed values for precipitation and stand age respectively

In comparison to loamy and sandy soils, organic soils contribute a significantly higher proportion of the relative soil C stock (Tab. 24). The upper limit of the 95% confidence interval of loamy soils is even less then the lower limit of organic soils.

Tab. 24. Basic statistics of relative soil carbon stocks distributed to soil category.

RELATIVE SOIL C (%)	**LSMean**	**95% confidence limits**	
		lower	**upper**
Loamy	61. 6 [a]	58.4	64.8
Organic	73.1 [b]	66.8	79.7
Sandy	64.8 [a]	62.5	67.1

Note: [a b] indicate significant differences within one group.

At rates with the lowest biodiversity, the relative soil C stock decreases with stand age. As soon as the biodiversity increases, the relative soil C stock increases with stand age (Fig. 15, bottom).

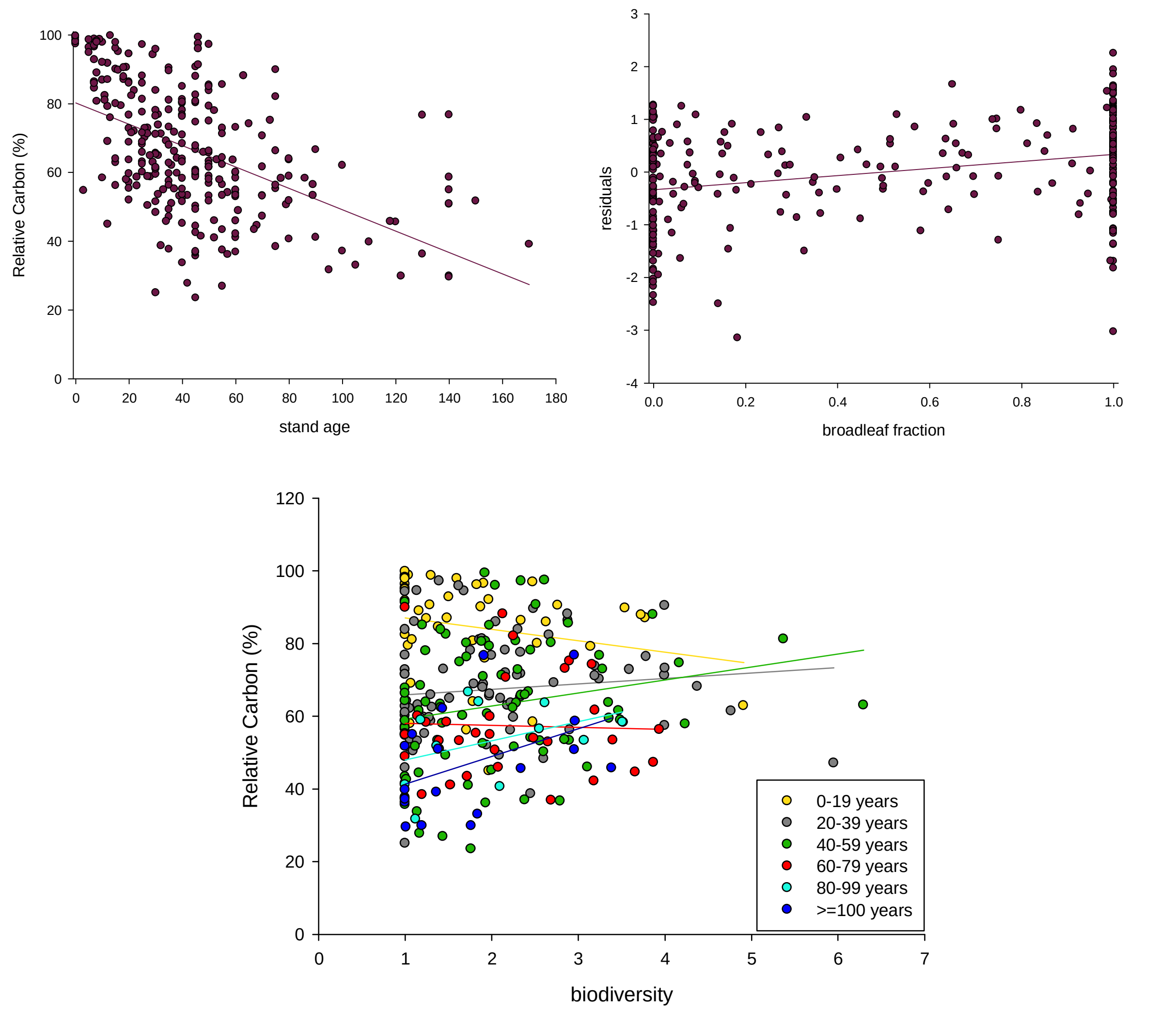


Fig. 15. Relative soil carbon by stand age (**top left**). Influences of broadleaf fraction on relative soil carbon stock after the effects of the variables before have been removed (stand age and crown cover). Shows how much is explained by the added variable on the X-axis (**top right**). Relative soil carbon stock as a function of biodiversity for different stand age classes (**bottom**).

6. Discussion

In comparison to the world's average forest C stock (162 t ha^{-1} (FAO 2010)) as well as to the world's temperature forest C stock (152 t C ha^{-1} (IPCC 2000)) , the C content in Danish forests is higher (279 t ha^{-1}). During the last approximately 10 years the above- and belowground biomass, the dead wood and the forest floor C pool in Danish forests have been increasing: Biomass C stock amounts to 36.9 million t in 2010, which is almost 1.5 times more than in the year 2000. The forest floor C stock increased by 1 million t to 6.8 million t in 2010, while the dead wood C stock shows a growth by 0.1 million t to 0.5 million t in 2010. Data for the soil C stock are not available for comparisons (FRA 2010). A study on the forest C pools in Wisconsin, U.S.A., reveal a total C stock of 252 t ha^{-1}, with an allocation of about 65% to the soil C pool, 22.7% to the biomass, 7.5% to the forest floor and 4% to the dead wood C stock (Wisconsin DNR n.d.). According to the U.S. Agriculture and Forestry Greenhouse Gas Inventory from 1990-2009 (U.S. Environmental Protection Agency 2011), most C is stored in above- and belowground biomass, accounting for 44.7% together, the second biggest amount is stored in the soil (38.0%). Forest floor and dead wood account for 10.7% and 6.75% each. The comparison is, however, difficult since different definitions of these pools are applied. For the latter study for instance, the living understory is included in the aboveground C pool. This might explain the higher biomass C stock compared to the soil. There are several possible explanations for the lower average world's C stock compared to Danish forests. First of all, the average C fraction globally used amounts 0.48, Denmark applies a C fraction of 0.50. Secondly, the average world's forest C stock does not represent 100% but 94% of the world's forest area. Moreover, the response of the countries to the C pools varied. Only 61% of all countries replied to the dead wood C stock and about 78% to the soil C stock. Thirdly, despite efforts of harmonization of national forest inventories, different forest definitions and soil sampling depth were applied (FAO 2010).

All but two independent variables examined in this study are significant for the absolute forest C stock in one way or the other. Tree species biodiversity and broadleaf fraction are only significant for the relative soil C stock. While precipitation and PLU significantly affect the forest floor only stand age, soil category, crown cover and tree species category constitute significant effects on three out of five C pools (including the total C stock). The amount of a single effect explaining the major variance in the total C stock decreases in the order stand age > soil category > crown cover > tree species category (Tab. 9).

6.1. Stand age

In general, the results supported the hypothesis that the total C stock as well as the biomass C raises with increasing stand age. Moreover, the same effect applies for the forest floor C stock. This can be attributed to varying photosynthesis and decomposition rates (Tyrrell et al. 2012). Older trees do not sequester as much C as younger trees which is explained by a slower growing rate. Nevertheless, older trees have a larger biomass in which the C has had more time to accumulate (Lorenz & Lal 2010). Other studies confirm this finding (e.g. Tyrrell et al. 2012). According to Pregitzer et al. (2008) (in Tyrrell et al. 2012), the C sequestration peaks within the age class of 11 to 30 years old stands. The results from this study indicate a peak in the C stock at stands between 35-60 years (Fig. 8, Fig. 9 and Fig. 11). The following stagnation phase becomes most visible within the **biomass** C stock (Fig. 9). In this pool, the two most important significant effects are stand age and crown cover, displaying the biomass production rate. In combination with crown cover, the influence of stand age is highest on younger to medium old stands and lowest on older stands. Logically, the **total** C stock has a higher potential to increase in younger stands with low crown cover than in older stands.

Stand age within **forest floor** C pool comes second after tree species category (Tab. 14), but third after precipitation in relative forest floor (Tab. 21). With increasing age, more leaves and other plant materials accumulate on the ground, leading to a steady input of organic matter over time. Therefore, depending on the tree species category and on the litter quality, more C is accumulated, too. Contrary to the stand age's effect on biomass and forest floor, the **relative soil** C stock decreases with increasing stand age since older stands contain more C in biomass than younger. Thus, the percentage of soil C decreases.

6.2. Soil category

The soil category is the most critical for the **soil** C stock, as initialliy hypothesized, but it also has a significant influence on the **biomass** C stock and of course on the **total** C stock (Tab. 16, 11 and 9). Overall, the high variation of the C content in the soil categories might be caused by the very heterogeneous plots (Rodeghiero et al. 2010). Within the **soil** and total C pool, the organic soil category has a significantly higher C stock than loamy and sandy soils which could mainly be attributed to its higher SOM content. The same might explain the minor difference between loamy and sandy soils. Both contain far less organic matter than the organic soil category whereas the variability of organic matter content in loamy and sandy soils indeed varies with samples but obviously to almost the same extent. Each soil category is characterized by its properties (e.g. clay content, pH, soil moisture). These in turn determine, among others (site conditions, litter input quality and quantity and its type of C compounds -labile or stable C), the turnover rate of SOM (Jandl et al. 2007). Soil respiration increases with soil temperature, hence the amount of SOM is lower in areas with higher temperatures. Yet, the turnover of SOM containing stable C is independent of temperature (Jandl et al. 2007). In general, low temperature and excess soil moisture surpress soil respiration. Furthermore, clay minerals and oxides enable C to form stable complexes, impeding mineralization of C (Jandl et al. 2007). Soil microbial processes are hindered in sandy soils and in soils where nutrient availability is low or with a low pH (Jandl et al. 2007).

Regarding the **biomass** C pool, the biggest C amount is stored on areas with loamy soils, followed by organic soils. Both differ significantly from sandy soils (Tab. 12). This could be explained by the influence of the tree species categories representing the site conditions. Meaning that the soil conditions influence which kind of species is growing best on the respective site. According to the total C stock, most C accumulates in broadleaf forests, least in conifer forests (Tab. 6). Approximately 66% of the plots on loamy soils are covered with broadleaf dominated forests of which about 50 % are located on loamy and 16% on organic soils. Conifer forests, instead, are largely located on sandy soils (83%). Hence, the biomass C stock on sandy soils is lowest. On the other hand, this distribution could occur no matter what tree species is growing on loamy, organic or sandy soils because the tree species are not equally distributed on the different soil categories. This is confirmed by the analysis of the **relative biomass** C stock. Here, conifer dominated forests contain the significantly biggest relative biomass C stock compared to mixed, broadleaf and temporarily unstocked stands (Tab. 19).

6.3. Crown cover

The crown area helps to determine the extent to which a tree is able to conduct photosynthesis since photosynthesis is mainly carried out via leaves. Consequently, increasing crown cover indicates a bigger amount of trees in the respective area. However, the same cover ratio can be composed of both a few old trees on the one hand, and multiple young trees on the other hand. Since younger trees contain less C than older ones, a high crown cover does not necessarily indicate bigger biomass C stocks. Nevertheless, the overall effect of increasing crown cover is positive for the **biomass** C stock. Additionally, crown cover extent also has a positive significant effect on the **total** C stock (Tab. 9).

The forest floor development depends on decomposition rates, hence on litter properties (e.g. C:N ratio), and disturbances such as heavy rain or strong wind events causing leaves or branches to fall down (Woodall et al. 2012). As the C accumulation in **forest floor** increases with forest floor development (Vesterdal et al. 2007), it is surprising that the crown cover does not have a significant impact on forest floor C stock. Penne et al. (2010) investigated the impact of the canopy structure of a pure pine stand on the spatial variability on forest floor C stocks and found out that only the mass of input material is crucial for the accumulation of C in the forest floor. While the canopy structure influences the litter fall, the mass reaching the ground affects the environmental conditions for microbial/enzymatic activity that determine the mineralization/decomposition.

As expected, the results for **dead wood** C content are not very representative and have to be carefully interpreted. Although crown cover had the single weakly significant effect on this C pool, the following has to be considered: First of all, there were relatively few sample plots (only 87 out of 277 contained dead wood), hence, the representativeness is lacking (Bradford et al. 2010). Secondly, the final model has a low coefficient of determination and is accordingly not very reliable. Thirdly, regarding the graphical analysis, the pattern for high crown cover can also be assigned to areas with lower crown cover (Fig. 10). As Nord-Larsen et al. (2008) indicate, the distribution of dead wood volume is highly dependent of the sample plot size. Thus, the assumption is having more sample plots with dead wood content, which might be achieved by extending the sample plot size, the C stock in dead wood might not significantly differ with varying crown cover. Additionally, the interaction of crown cover and tree species category might not be relevant for dead wood either. Instead, dead wood C stock is expected to depend on stand age. This can be attributed to the senescence process of trees since it leads to e.g. more input of woody debris (Lombardi et al. 2008; Lorenz & Lal 2010). Moreover, the dead wood volume increases with the frequency and intensity of disturbances (Christensen et al. 2003). In addition to the above mentioned factors, forest type and species composition as well as local soil and climatic conditions influence the decomposition and therefore affect the C stock of dead wood (Lombardi et al. 2008). Calculating dead wood C stock, the different constitution of wood of conifer and broadleaves (hard- and softwood proportion) has to be considered determining the decomposition factor (Brown 2002).

The **relative soil** C stock decreases with increasing crown cover for the same reason as it declines with increasing stand age. Higher crown cover indicates more biomass C. Therefore the soil C pool shows a smaller percentage in the total C stock.

6.4. Tree species category

As hypothesised, the tree species significantly affect the C stocks of the forest floor, soil and the total C stock (Tab. 14, 16 and 9). Due to the different growing patterns, meaning the different increase in biomass volume over the years as well as heart- and sapwood contents of broadleaf and conifer trees it was expected that their different C stocks have a significant influence on the total biomass C stock. This is, however, not the case. In addition to the variables stand age and crown cover that are explaining the development of biomass volume, the soil category is significant. The soil type sets the conditions for species to survive and grow on that specific site as well as influencing the vegetation productivity (Baritz et al. 2010). Therefore, the tree species category is still addressed to a certain degree in the absolute biomass C stock. The tree species effect is eventually revealed in the relative biomass C stock.

Regarding the **forest floor** C stock, the tree species category constitutes the main significant effect. The litter of conifer trees for instance contains more lignin than that of broadleaved trees and is thus more resistant to decomposition. Consequently, more litter accumulates on the ground and the forest floor layer becomes thicker. The main influence of tree species on the forest floor C stock is derived from the varying turnover rates (Vesterdal et al. 2008). This could also explain the higher forest floor C content under mixed stands. Eight plots with broadleaved forests (consisting of beech and oak dominated stands) constitute an exception. Since all plots are located on sandy (7) or loamy (1) soils, an underlying effect of soil category on forest floor C stock might be expected (higher on sandy and loamy soils than on organic soils). This is also confirmed by the fact that a higher percentage of conifer species than broadleaved is situated on sandy and loamy soils. Unlike Tyrrell et al. (2012) stated, in this survey the C pool differs significantly with tree species category. The interaction of stand age and tree species category indicate that besides the single effects of these variables, the combination of e.g. old stands dominated by broad-leaved trees still store significantly less forest floor C than conifer stands of the same age. Moreover, coniferous species have a shallow root system leading to higher accumulations of SOM in the forest floor than in the mineral soil (Jandl et al. 2007).

Whether forests are dominated by conifer or broadleaved trees also influences the **soil** C stock significantly. In contrast to a study from Wisconsin (Wisconsin DNR n.d.), the results from this study show that most C is stored in soils under broadleaved forests (Tab. 17). Firstly, this effect can be attributed to the different litter quality and quantity, leading to a different SOM quality (Thuiller et al. 2006). The litter quality determines whether microbes can decompose it easily or if it is more resistant. In general, C allocation to roots and consequently, the SOC content increases with rising litter input (Raich & Nadelhoffer 1989) and forest productivity combined with unfavourable decomposition conditions (Baritz et al.2010). Secondly, it can be explained by the different root development, quality and finally root decay rates of conifers and broadleaves (Vesterdal et al. 2008), which is, however, also depending on the soil (Silver & Miya 2001). Moreover, C is released to the soil via root-associated symbionts which may not only differ by tree species category but also by soil category. However, these results may as well be caused by the uneven distribution of forest types over the soil categories thereby only mirroring the already discussed effects of soil categories on soil C stocks. In agreement with a study by Vesterdal et al. (2008), species with low forest floor C, contain more C in the soil (Tab. 15 and Tab. 17).

The **total** C stock surprises by the clear difference between broadleaved and conifer forests. Forests dominated by broadleaved trees store in total more C (Tab. 10). Only the forest floor C stock has a higher C content in conifer forests (Tab. 15). Since tree species set different conditions to their environment which is expressed in varying tolerances of the site conditions (e.g. conifers grow on lower pH than broadleaves), species occupy different ecological niches, and hence they can complement each other (Jandl et al. 2007). Therefore, mixed forests have higher biomass production and C stock than those dominated by conifers. As the soil C stock, attributing the highest C stock to broadleaf forests, contributes the most to the total C stock, it is likely that these forest types show the highest C stock in total (after combing all C pools) as well. However, as discussed above, the high total C stock in broadleaf forests can be attributed to the uneven distribution of forest types over the soil categories resulting in higher soil C stock under broadleaf forests. Moreover, it can be attributed to the higher average stand age of broadleaves compared to conifers (see Chapter 6.9).

The results for the single tree species rather give indications about the C allocation than being reliable. In order to get reliable results the sample size need to be larger. Moreover, pure stands of a specific tree species need to be sampled to further strengthen the validity of the results. Nevertheless, the results for C allocation under single tree species in this study mostly confirm those of the tree species category, e.g. the fact that forest floor C stock under conifer dominated stands is higher than under broadleaf trees, is confirmed by the single conifer tree species (Tab. 15).

6.5. Precipitation

The effect of precipitation is only significant for the **forest floor** C stock. Heavy rainfalls, ice and snow contribute to litter input to forest floor and the soil (Lorenz & Lal 2010). As Baritz et al. (2010) points out, a prolonged water-saturation of the top soils impede decomposition, hence resulting in a thicker forest floor layer, containing more C. In Denmark, however, the precipitation range is too low to result in prolonged water-saturation. This might rather be an aspect of topography. On the other hand, Lensing & Wise (2007) suggest that increased leaching and growth of microflora might explain the accelerated decay rate in case of increased rainfall. However, precipitation could also be an effect displaying the growth of the stand.

Moreover, it has to be mentioned that the effect of precipitation could cover the impact of soil category. If the variable of precipitation is left out, the soil category entered the model. According to the precipitation pattern, it is highest in western Denmark. In addition, most sandy soils are located in western Denmark and on sandy soils in turn, grow mostly conifer forests. This again represents the effect of the tree species category with highest forest floor C stocks under conifer forests.

6.6. Previous land use

Previous land use affects only the **forest floor** C stock to a significant extent. The reference year for PLU is 1990. Forests remaining as forests beyond this date still have a significantly higher forest floor C stock than afforested areas. Thus, the C content in the forest floor increases consistently as the forest floor develops (Jandl et al. 2007). This is also confirmed by a study of C sequestration in soil and biomass following afforestation carried out by Vesterdal et al. (2007).

It could have been expected that also the forest **soil** C stock is influenced by the previous land use. Comparing the soil C stock of arable land and forests, it leads to the conclusion that PLU affects soil C sequestration and storage since forest soils contain more C (Vesterdal et al. 2009). In addition, it has been reported that the soil C content following deforestation declines (Vesterdal et al. 2007; Jandl et al. 2007). Therefore, it has been inferred that afforestation measures on arable land would increase soil C as well as forest floor C stock –if afforestation took place on nutrient-poor sandy soils (Vesterdal et al. 2007). Nevertheless, planting can induce the mineralization of SOM evoking to C losses if they are not offset by litter fall (Jandl et al. 2007). As PLU is not a significant factor for soil C pool even so, it could be related to the time span, explaining that after a maximum of 20 years after the afforestation took place (which was in 1990) no significant difference is detectable anymore.

6.7. Broadleaf fraction

Regarding the **relative soil** C stock, not the tree species category but the broadleaf fraction is significant. The increase in relative soil C stock with an increasing content on broadleaf trees shows that the amount of broadleaf trees is more important than the single tree species category. This result supports the result of the absolute soil C stock, indicating that soils under broadleaf trees contain more C than those under conifer or mixed stands. A higher percentage of soil C under broadleaf forests means that at the same time, the other C pools are relatively smaller. Consequently, this reveals that conifer forests, which have a smaller percentage of soil C than broadleaved forests, have a bigger percentage of e.g. forest floor C.

6.8. Biodiversity

Biodiversity has a significant effect on the **relative soil** C pool only. Younger and less diverse stands store more C than older stands with the same low biodiversity rate. On the whole, the relative soil C stock of more diverse stands increases with stand age. Forests that are used for harvesting are probably cut more often than unmanaged forests and are dominated by single species. This results in generally younger, less diverse stands that have a higher percentage in soil C, whereas unmanaged stands may be more diverse and relatively older, containing less relative soil C but more C in biomass.

6.9. Other factors

Besides those factors examined in this study, the C stock in forests is influenced by several other factors. Regarding the total C stock, another argument for the high C stock in broadleaf forests is the generally older broadleaf stands. Especially beech dominated forests show a relatively high average age (Tab. 7). The age of the different stands could be influenced by the wood market for instance. Regarding old beech stands, this would indicate a bad market situation/ low prices for beech wood. Consequently, beech stands were not cut but maintained and conifer stands have in general a shorter rotatoin rate. The average young age for conifer forests could also be a result of windthrows. As their root system is rather swallow, they are more prone to windthrows than broadleaf trees. In combination with crown cover, conifer and mixed forests show a higher influence on total C stock than broadleaf forests (Fig. 8). This might also be explained by the fact that broadleaf forests are on average older than the other two categories, hence, the average total C stock is higher regardless the crown cover extent.

Besides the natural factors (e.g. senescence process), the management of a forest has the main influence on dead wood volume and consequently, on C stock. In general, dead wood volume is higher in unmanaged than in managed forests (Lombardi et al. 2008). A slight indication of that founding by Lombardi et al. (2008) within the results of this study might be derived from the distribution of dead wood C between the tree species categories (Tab. 13). In comparison to conifer and broadleaf dominated forests, mixed forests contain most dead wood C. Plantation forests that are used for wood production, and thus fall into the category of managed forests, mainly contain the same species. Therefore, they are either classified as conifer or as broadleaf stands. As a result, this might support the fact that managed forests contain less dead wood C.

Forest management can also influence the soil C stock. An increased productivitiy leads to an increased amount of C allocated to the soil. However, tree species affect the rate of how much C accumulates and how it is distributed within the soil. Mixed forests show less high rates of SOM decomposition and contribute to the forest's stability. In general, C losses are reduced when disturbances in the stand structure and the soil are kept to a minimum (Jandl et al. 2007).

Moreover, concentrations of Ca and P as well as the pH affect the decomposer system and thus the accumulation of C in forest floor and soil. The increasing soil nutrient status causes the forest floor C content to decrease. However, different pH and C/nutrient ratios in forest floor under various tree species may be related to their genetically different litter quality, which in turn supports the result of the forest floor C model indicating the significant influence of the tree species category (Vesterdal & Raulund-Rasmussen 1998).

6.10. Statistical considerations

The automatic selection procedure of the "best fitted" regression model has its constraints. It is criticized that the statistical rules for deciding the entrance and removal threshold of each variable to the model are somewhat randomly chosen within this process (Quinn & Keough 2002). Moreover, statistical hypothesis testing and the significance levels or the *F* statistics are not well suited for this procedure. There is a risk of "overfitting" the model, occurring when some predictor variables are added to the model since they yield a higher r^2 but at the same time adding only slightly more to the explanatory power. Therefore, the chosen variables in the final model might not be always related to the response variable. Moreover, collinearity between the predictor variables influences the selection process (Quinn & Keough 2002; SAS Institute Inc. n.d. b).

However, efforts to avoid these constraints have been made by testing for collinearity of predictor variables before running the model. Further, the model results have been checked for validity by graphical analysis. This has been done by creating a sequence of residual plots, including a procedure of added variable testing (see Appendix V and VI).

In total, addressing the soil category and tree species category as well as single tree species and PLU, some results are rather weak. The representation of conifer and mixed forests on organic soils for instance is small (Tab. 6 and Tab. 7). The same is true for afforested (AFF) sites.

7. Conclusion

Since forests are of profound importance to the global C cycle, reporting on forest C is fully reasonable. Firstly, changes can be detected, secondly, factors influencing C storage can be determined and finally, efforts in forest management promoting C storage can be adapted respectively. The C trading might give incentives to developing countries, where the main deforestation occurs, to make more efforts to maintain and expand their forests. In comparison to the world's temperate forest C stock, the study results indicate a higher C accumulation in Danish forests. A combination of a further extension of Denmark's forest area with efforts to increase the existing C stock is not only beneficial for the nation's GHG balance but also for the world in general.

The overall expectation that, at least in temperate forests, two-thirds of the total C stock is located in the soil could be confirmed in this study. The most significant variables on the total C stock are mainly those affecting biomass volume (stand age and crown cover) and its composition (different lignin and hardwood content of different tree species). Moreover, a significant effect on the total C pool can be attributed to the soil category. As assumed, the effect of soil category on C accumulation in biomass displays the impact of tree species. In contrast to the general observations this study showed that broadleaf forests have a bigger C stock than conifer forests. This, however, might be attributed to an uneven distribution of forest types on soil categories or to the fact that conifer forest stands were in this study generally younger than broadleaved stands. Other factors influencing the biomass C stock might derive from the industry and market prices for wood.

The result for dead wood C pool is not representative since there were too less samples. Besides, the age and the previous land use is determining the forest floor C stock. This indicates a high potential in the overall forest floor C stock to show a net increase in the future, provided that the forest area/ average stand age also increases. The assumption that the PLU also significantly influences soil C stock is not confirmed. However, not only the soil category but also the tree species category affect the soil C stock. On the whole, both the dead wood C stock and the soil C stock are influenced by forest management strategies.

All in all, this study gives a broad overview about the C content in Danish forests as well as about some selected influencing factors. In order to estimate the influence of single tree species, a study area with forests dominated by the respective specie has to be set up. The comparison of forest C inventories in general, is only possible if the sampling design is the same. Moreover, the utilization of this explanatory model as a predictive model for absolute and relative C stocks is subject to restrictions. The application in other countries and under site conditions different to this study has to be further examined. Finally, the extend to which forests can store C is mostly unknown. At some point the C sinks might be saturated and enter a state of equilibrium.

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Appendix

Appendix I: List of Variables and Measurement Units

Tab. 25. List of variables (Variables, Abbreviation, Description, Unit)

Variable		Description	Unit
PSU		5000 primary sampling units located in a 2x2 km grid, out of which 277 sampling plots have been randomly collected.	-
SSU	A, C, E, G	Secondary sampling plots, with a forest cover of >50%.	-
TSU	1, 2, ...	SSU plot that has further been subdivided due to different land uses or tree species.	-
Sampling Year	2007-2011	The year a plot was sampled.	(year)
Total Carbon Stock		Adding up biomass, dead wood, forest floor and mineral soil carbon.	t ha^{-1}
Biomass Carbon		Amount of carbon above- and belowground.	t ha^{-1}
Dead Wood Carbon		Amount of carbon stored in dead wood.	t ha^{-1}
Forest Floor Carbon		Amount of carbon stored in forest floor.	t ha^{-1}
Mineral Soil Carbon		Amount of carbon stored in mineral soil.	t ha^{-1}
Soil category		The type of soil. The description of the soil has been made according to the GEUS_25 soil map. As the GEUS_25 only has coverage of 85% of Denmark's land area, the GEUS_200 map has been used for missing data.	(Category)
	Loamy	Soil types with the code: • DL ML (GEUS_25); Marine deposits of sand and clay (→"Marint sand og ler"), • Clayey till (→"Moræneler"), Glaciofluvial deposits of clay (→"Smeltevandsler") (GEUS_200).	
	Organic	Soil types with the code: • FP FT (GEUS_25); • Freshwater sediments (→"Ferskvandsdannelser") or Marsh	

		(→"Marsk") (GEUS_200).	
	Sandy	Soil types with the code: • ES HS TG TS TS-TG YS S DG DS MG MS (GEUS_25); • Extra-marginal deposits (→"Extramarginale aflejringer"), Glaciofluvial deposits of sand and gravel (→"Smeltevandssand og -grus"), Sandy-gravelly till (→"Morænesand og grus"), Prequa-ternary (→"Prækvartær"), Older ma-rine sediments (→"Ældre hava-flejringer"), Drifting sand (→"Flyvesand") (GEUS_200).	
Single Tree Species		Dominant tree species in each sampling plot. • Ash, Beech, Fir, Larch, Nordmann Fir, Norway Spruce, Oak, Pine, Sitka spruce	(Category)
Tree Species Category		Dominant tree category in each sampling plot.	(Category)
	Conifer	Conifer forest if >75 % dominance.	
	Broadleaf	Broadleaf forest if >75 % dominance.	
	Mixed	Mixed broadleaf and conifer forest if <75 % dominance.	
	Temporarily un-stocked	No trees, but still part of a forest or trees with DBH < 1.3m.	
PLU		Previous land use (i.e. land use in 1990).	(Category)
	FRF	Forest remaining forest.	
	AFF	Afforestation since 1990.	
Stand Age		Average age of trees in each sampling plot.	(year)
Crown cover		Proportion of canopy in each sampling plot.	%
Broadleaf fraction		Proportion of deciduous trees in each sampling plot.	%
Biodiversity		Measurement of biological diversity, using the Simpson index.	(Index)

Precipitation	The annual mean precipitation (one value for the years 2001 to 2010).	mm

Appendix II: Basic statistics for relative C stocks

Tab. 26. Basic statistics for relative carbon stocks.

Relative Carbon Stock	Number of plots	Mean	Std.Err.	95% confidence limits		min.	max.
				lower	upper		
Biomass	267	27.41	1.05	25.34	29.48	0	73.53
Dead wood	277	0.38	0.06	0.27	0.5	0	8.19
Forest floor	277	6.63	0.46	5.73	7.53	0.22	44.02
Soil	277	66.56	1.11	64.37	68.75	23.47	99.78

Appendix III: Distribution of total C stock to single tree species

Tab. 27. Basic statistics of total carbon stocks distributed to single tree species

Total C ($t\ ha^{-1}$)	LSMean	95% confidence limit	
		lower	upper
Ash	317	242	414
Beech	284	246	329
Fir	308	248	381
Larch	279	225	348
Nordmann fir	265	199	352
Norway spruce	272	236	313
Oak	252	21	296
Pine	220	188	258
Sitka spruce	279	235	331

Appendix IV: Original model result for absolute dead wood C stock

Tab. 28. Model results for dead wood carbon stock: significant effects influencing dead wood carbon stock, $\log_e$-transformed (n=87).

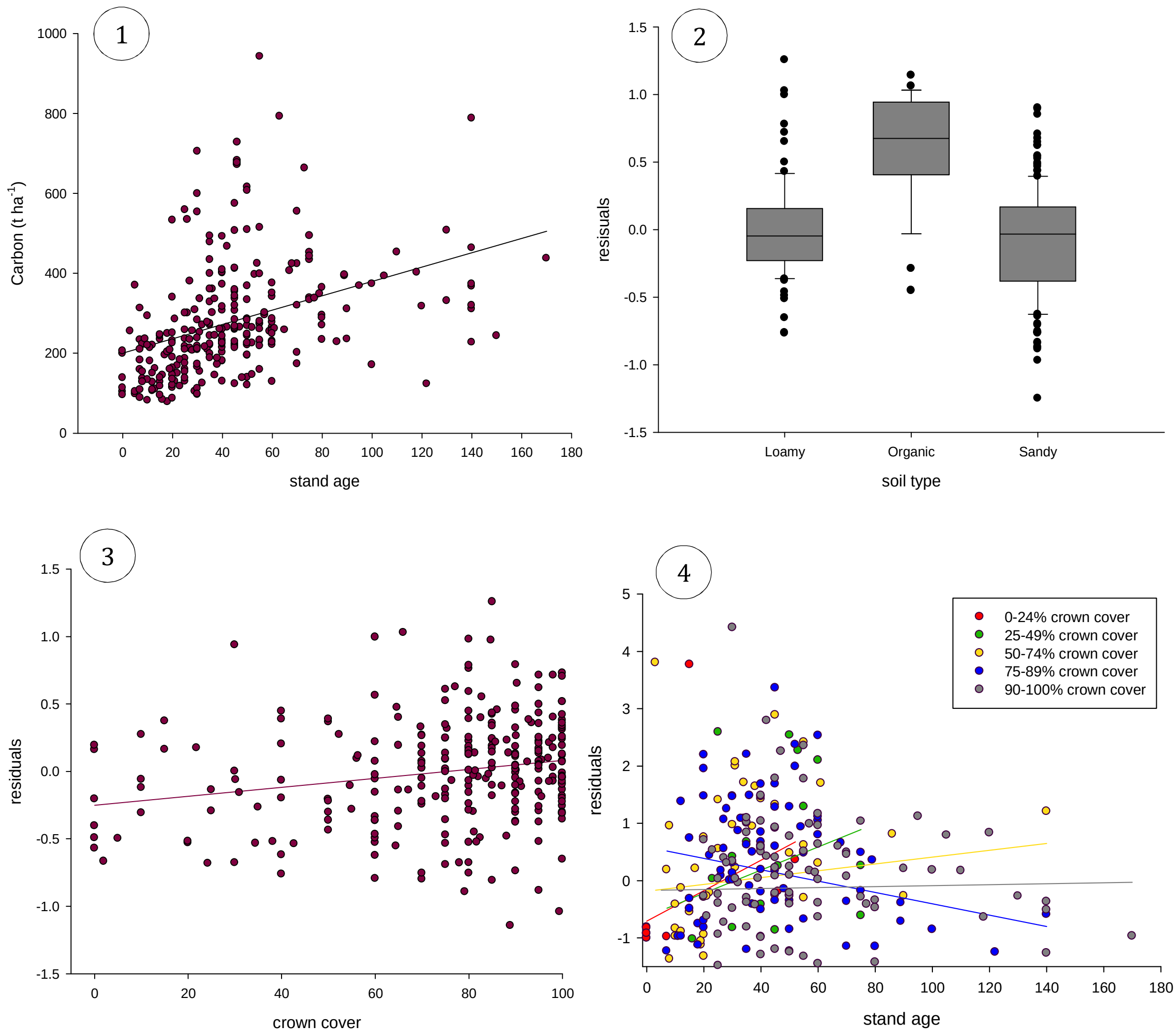
	FINAL MODEL: $\log_e$ DEAD WOOD C	p-value	r²	parameter estimate
I	intercept			1.796979696
A	crown cover	0.0422	0.047647	-0.014591626

Dead Wood Carbon= I+a·A

a = observed value for crown cover

Appendix V: Residual plots for total C stock and each absolute C pool

- **Total Carbon Stock**



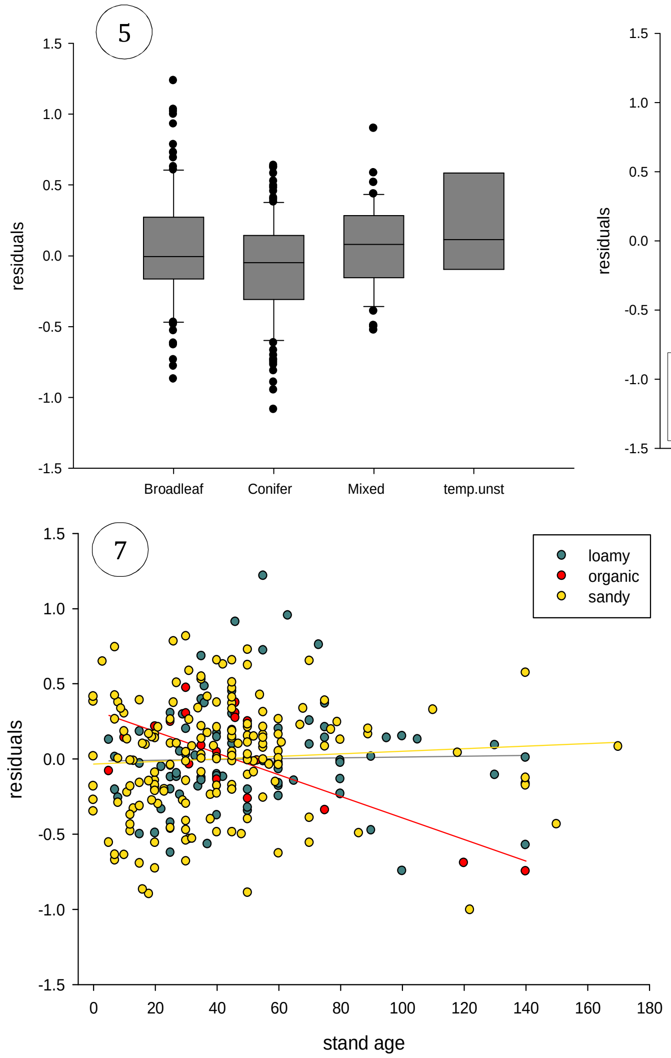
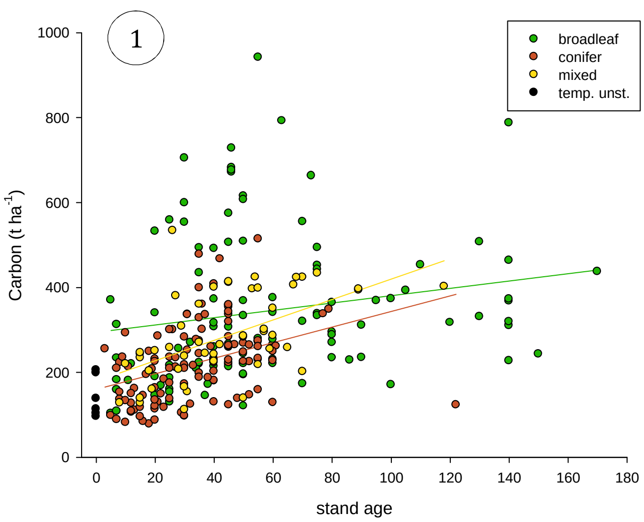


Fig. 16. Influences of each significant variable on total carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: stand age. 2. effect: soil category (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown). 3. effect: crown cover. 4. effect: stand age*crown cover (classes). 5. Effect: tree species category. 6. effect: interaction of crown cover * tree species category. 7. effect: interaction of stand age and soil category.



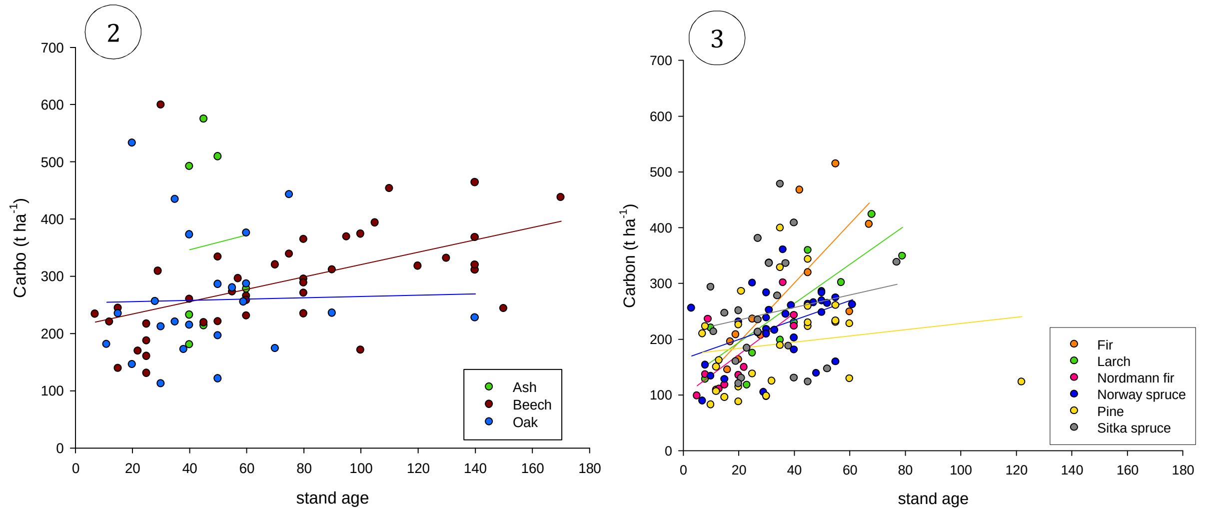


Fig. 17. Total carbon stock by stand age and tree species category. (1) and stand age and single tree species ((2)= broadleaf species; (3)= conifer species). As no clear pattern is detectable, this interaction has no significant influence on total carbon stock.

- ## Biomass Carbon Stock

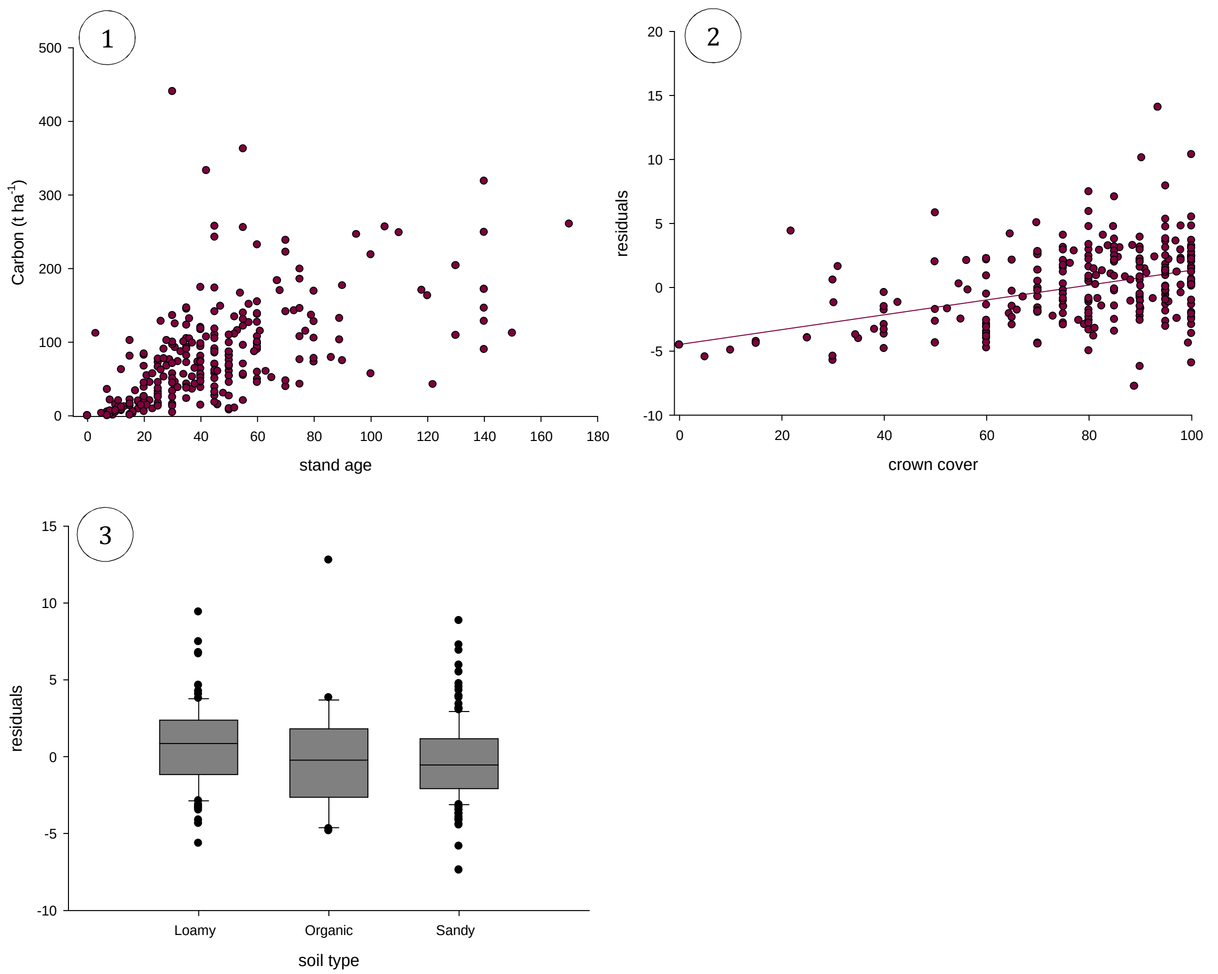


Fig. 18. Influences of each significant variable on biomass carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: stand

age. 2. effect: crown cover. 3. effect: soil category (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

- ## Forest Floor Carbon Stock

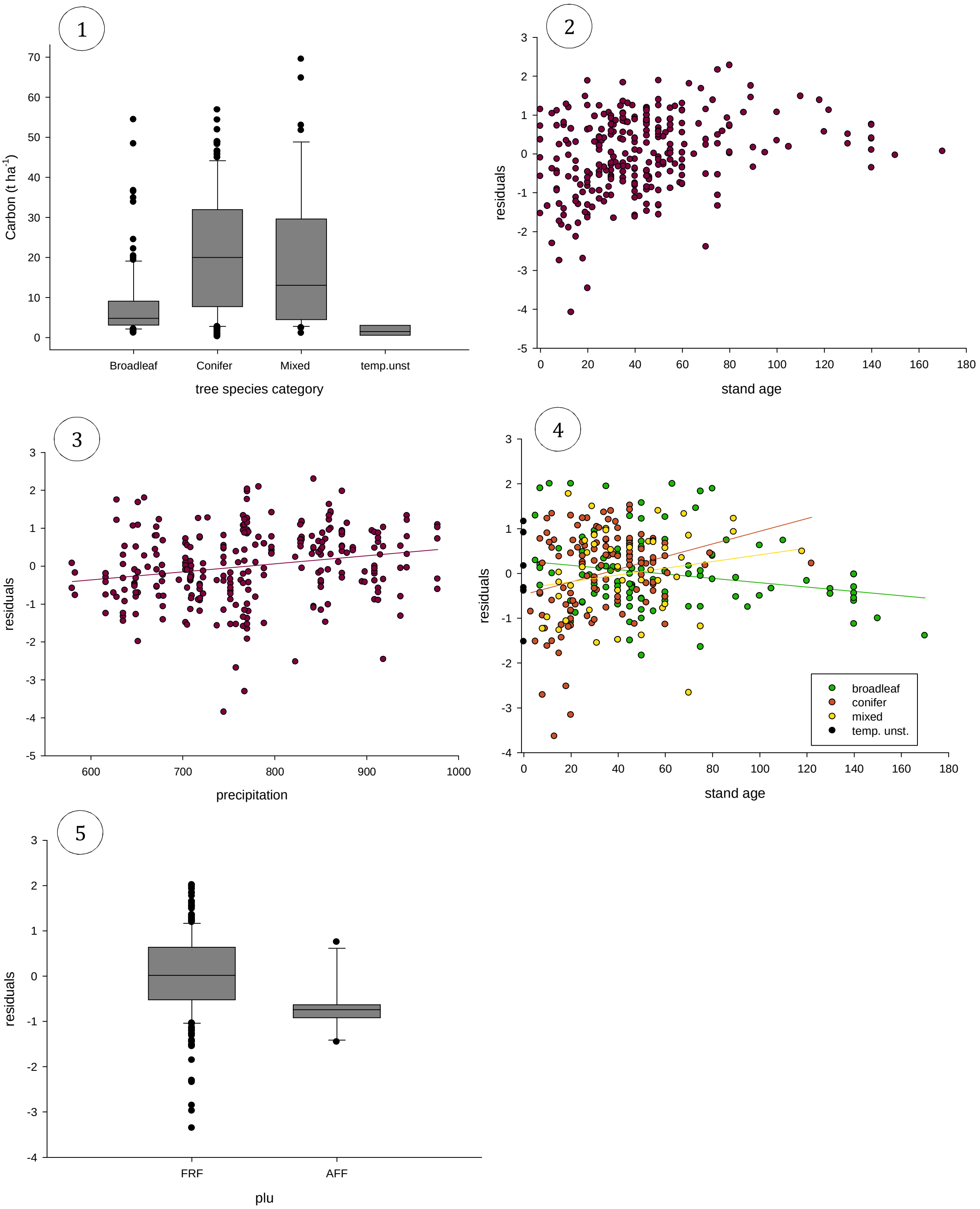


Fig. 19. Influences of each significant variable on forest floor carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: tree species category. 2. effect: stand age. 3. effect: precipitation. 4. Effect: interaction of stand age * tree

species category. 5. effect: previous land use (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

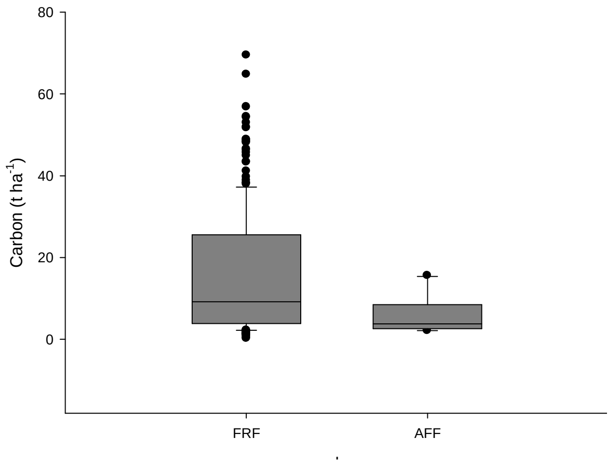


Fig. 20. Distribution of forest floor carbon by previous land use (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

- **Soil Carbon Stock**

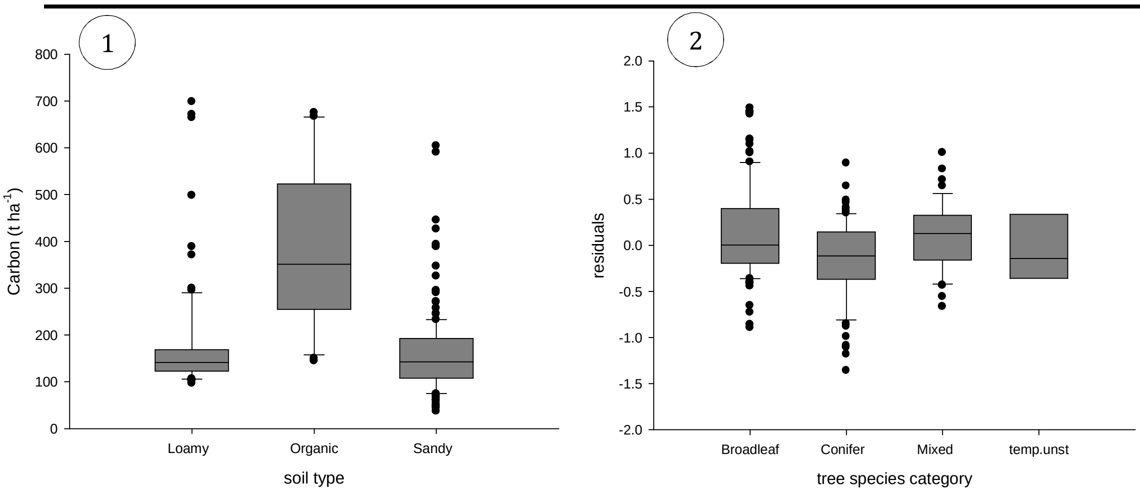


Fig. 21. Influences of each significant variable on soil carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: soil category. 2. effect: tree species category (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

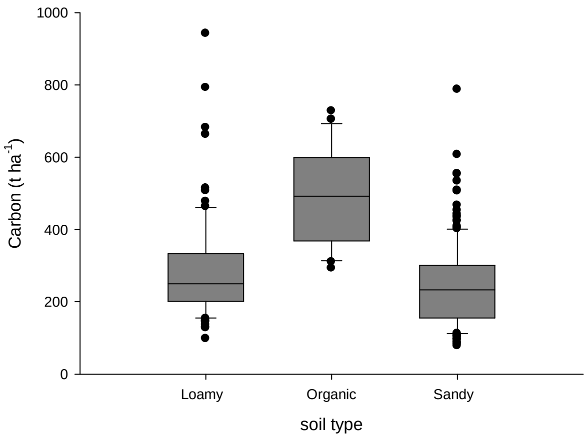


Fig. 22. Distribution of total carbon by soil categories (**bottom**) (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

Appendix VI: Residual plots for each relative C pool

- **Relative Biomass Carbon Stock**

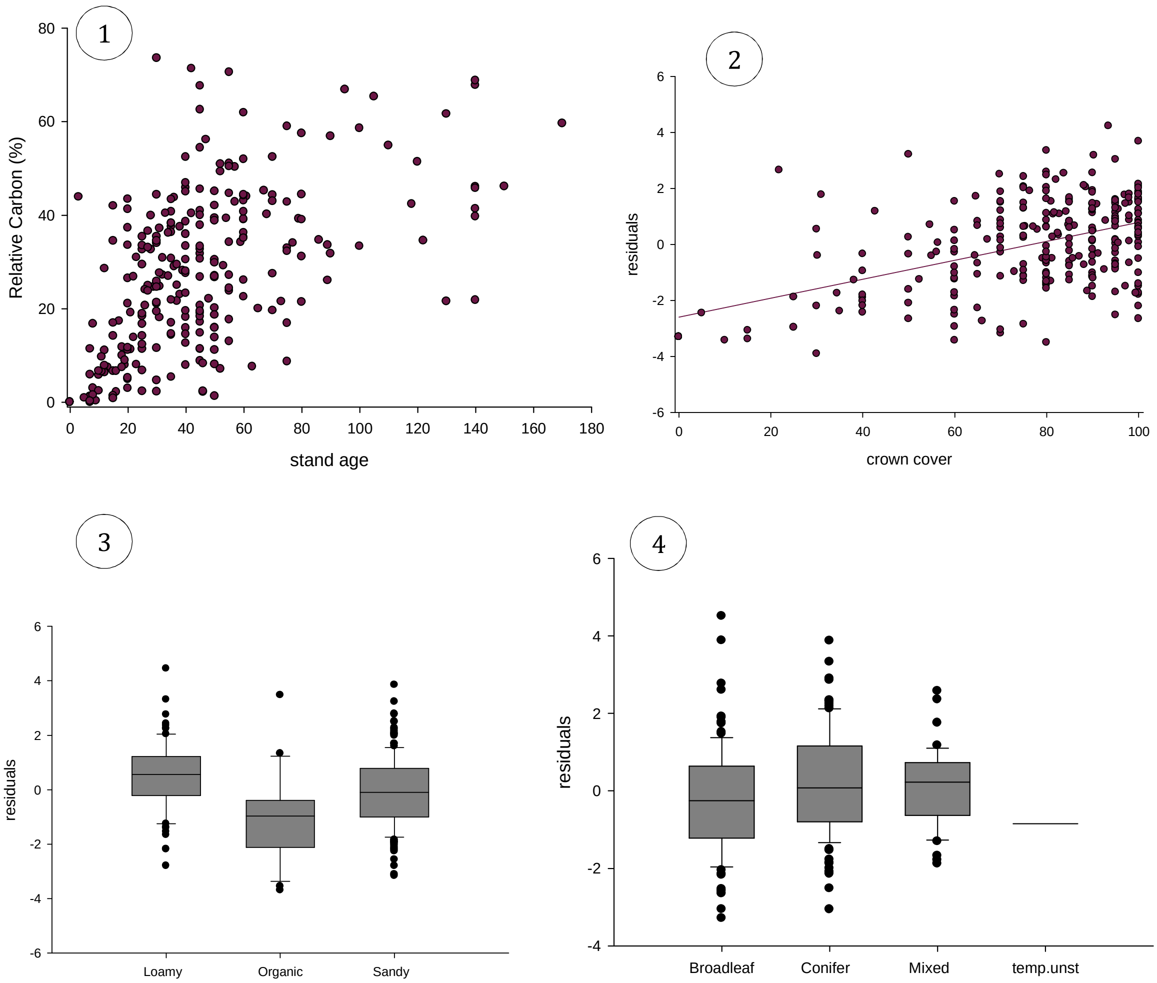


Fig. 23. Influences of each significant variable on relative biomass carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: stand age. 2. effect: crown cover. 3. effect: soil category (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown). 4. effect: tree species category.

- ## Relative Forest Floor Carbon Stock

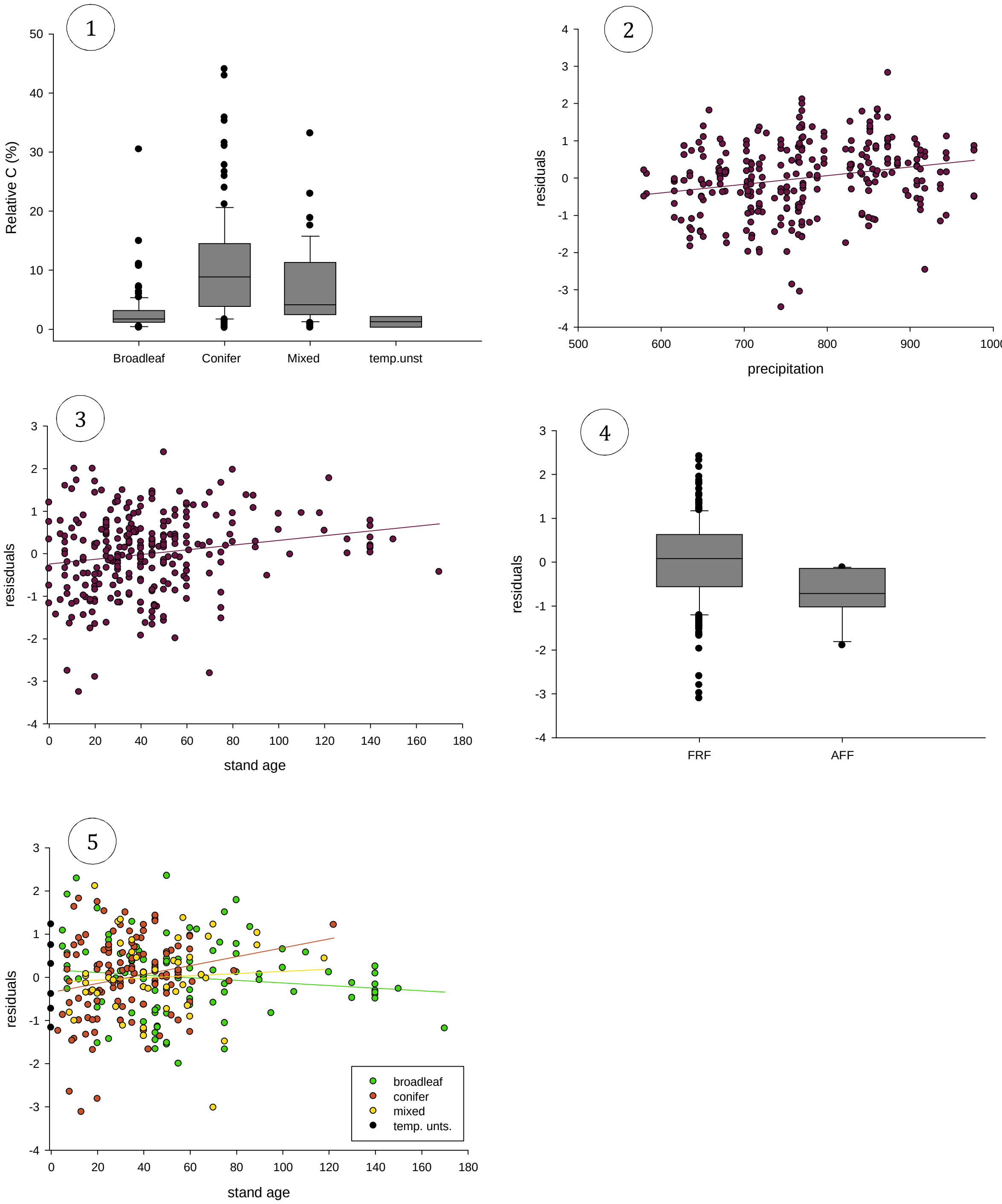


Fig. 24. Influences of each significant variable on relative forest floor carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: tree species category (here: the median, the interval of 25% to 75% (box) and minimum and maxi-

mum values are shown). 2. effect: precipitation. 3. effect: stand age. 4. effect: PLU. 5. effect: stand age*tree species category.

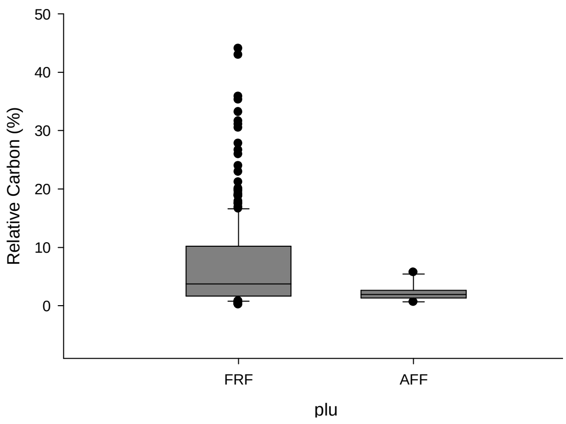
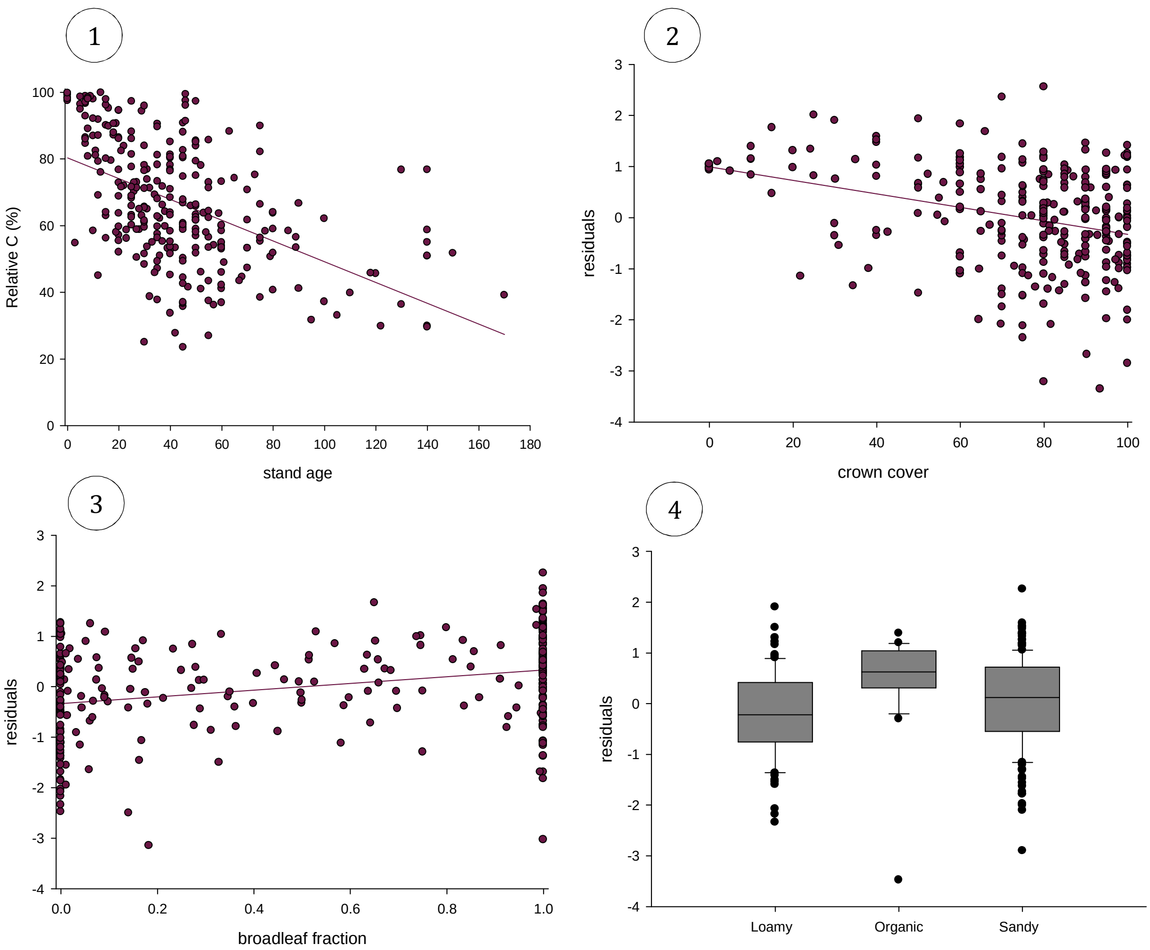


Fig. 25. Distribution of relative forest floor carbon by previous land use (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown).

- **Relative Soil Carbon Stock**



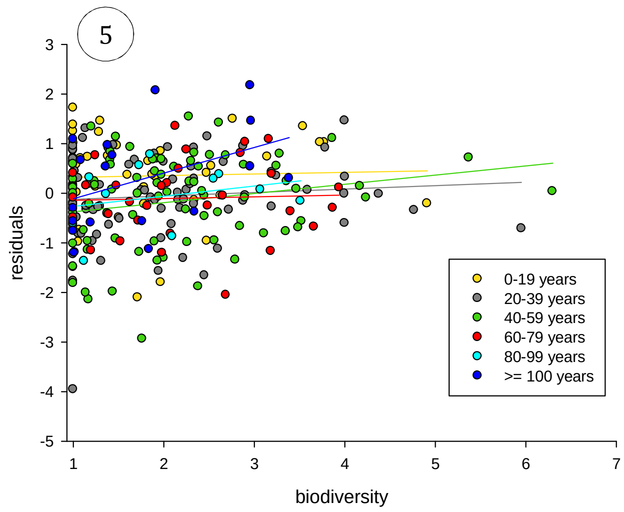


Fig. 26. Influences of each significant variable on relative soil carbon stock after the effects of the variables before have been removed. Shows how much is explained by the added variable on the X-axis. 1. effect: stand age. 2. effect: crown cover. 3. effect: broadleaf fraction. 4. effect: soil category (here: the median, the interval of 25% to 75% (box) and minimum and maximum values are shown). 5. effect: biodiversity*stand age (classes).

Appendix VII: Mean values for categorical variables for each carbon pool

Tab. 29. Basic statistics for total carbon stock; for each categorical variable.

TOTAL CARBON STOCK (t ha^{-1})	Number of plots	Mean	Std. Err.	95% confidence limits lower	95% confidence limits upper	min.	max.
Conifer	114	221	8.48	204	238	78.4	514
Broadleaf	110	344	16.3	311	376	103	941
Mixed	47	285	15.0	254	315	111	533
Temp. unst.	6	142	19.8	91.8	193	95.9	205
Loamy	82	288	16.0	256	320	98.1	942
Organic	23	482	28.7	422	541	293	728
Sandy	172	248	8.89	230	265	78.4	787
PLU FRF	267	279	8.65	262	296	78.4	942
PLU AFF	10	271	53.5	150	392	139	705

Tab. 30. Basic statistics for biomass carbon stock; for each categorical variable.

BIOMASS CARBON STOCK (t ha^{-1})		Number of plots	Mean	Std. Err.	95% confidence limits lower	95% confidence limits upper	min.	max.
	Conifer	109	65.9	5.86	54.2	77.5	0.48	362
	Broadleaf	107	100	7.55	85.0	114	0.03	440
	Mixed	45	84.6	8.34	67.8	101	1.89	222
	Temp. unst.	6	0	0	-	-	0	0
	Loamy	80	104	8.26	88.0	121	0.03	362
	Organic	22	81.9	19.5	41.3	122	3.41	440
	Sandy	165	69.9	4.79	60.4	79.3	0	333
PLU	***FRF***	257	82.4	4.39	73.7	91.0	0	440
PLU	***AFF***	10	51.2	13.0	21.8	80.6	1.89	140

Tab. 31. Basic statistics for dead wood carbon stock; for each categorical variable.

DEAD WOOD CARBON STOCK (t ha^{-1})		Number of plots	Mean	Std. Err.	95% confidence limits lower	95% confidence limits upper	min.	max.
	Conifer	114	0.71	0.15	0.41	1.01	0	10.33
	Broadleaf	110	1.55	0.39	0.77	2.32	0	22.7
	Mixed	47	1.50	0.51	0.47	2.52	0	20.4
	Temp. unst.	6	0	0	-	-	0	0
	Loamy	82	1.08	0.35	0.38	1.78	0	22.7
	Organic	23	1.77	0.56	0.60	2.93	0	8.82
	Sandy	172	1.12	0.24	0.64	1.60	0	21.1
PLU	***FRF***	267	1.17	0.20	0.79	1.56	0	22.7
PLU	***AFF***	10	0.81	0.44	0.19	1.80	0	4.32

Tab. 32. Basic statistics for forest floor carbon stock; for each categorical variable.

FOREST FLOOR CARBON STOCK (t ha^{-1})		Number of plots	Mean	Std. Err.	95% confidence limits lower	upper	min.	max.
	Conifer	114	21.1	1.39	18.4	23.8	0.24	56.8
	Broadleaf	110	8.34	0.89	6.56	10.1	1.16	54.4
	Mixed	47	19.5	2.58	14,3	24.7	1.11	69.47
	Temp. unst.	6	1.83	0.58	0.34	3.32	0.28	4.14
	Loamy	82	8.26	0.86	6.54	9.98	1.11	34.9
	Organic	23	12.3	2.29	7.59	17.1	1.75	36.40
	Sandy	172	19.1	1.24	16.65	21.6	0.24	69.5
PLU	***FRF***	267	183	0.91	13.9	17.5	0.24	69.5
PLU	***AFF***	10	5.90	1.53	2.44	9.36	2.17	15.6

Tab. 33. Basic statistics for soil carbon stock; for each categorical variable.

SOIL CARBON STOCK (t ha^{-1})		Number of plots	Mean	Std. Err.	95% confidence limits lower	upper	min.	max.
	Conifer	114	136	5.14	126	146	36.6	347
	Broadleaf	110	237	15.9	206	268	74	698
	Mixed	47	183	10.1	162	203	73.3	388
	Temp. unst.	6	140	19.6	90.4	191	95.6	201
	Loamy	82	177	13.0	151	203	96.7	698
	Organic	23	390	35.4	316	463	145	675
	Sandy	172	160	6.57	147	173	36.6	604
PLU	***FRF***	267	183	7.34	169	198	36.6	698
PLU	***AFF***	10	213	55.0	88.8	338	105	675

Appendix VIII: Soil types (GEUS_200 map and definition of soil type codes)

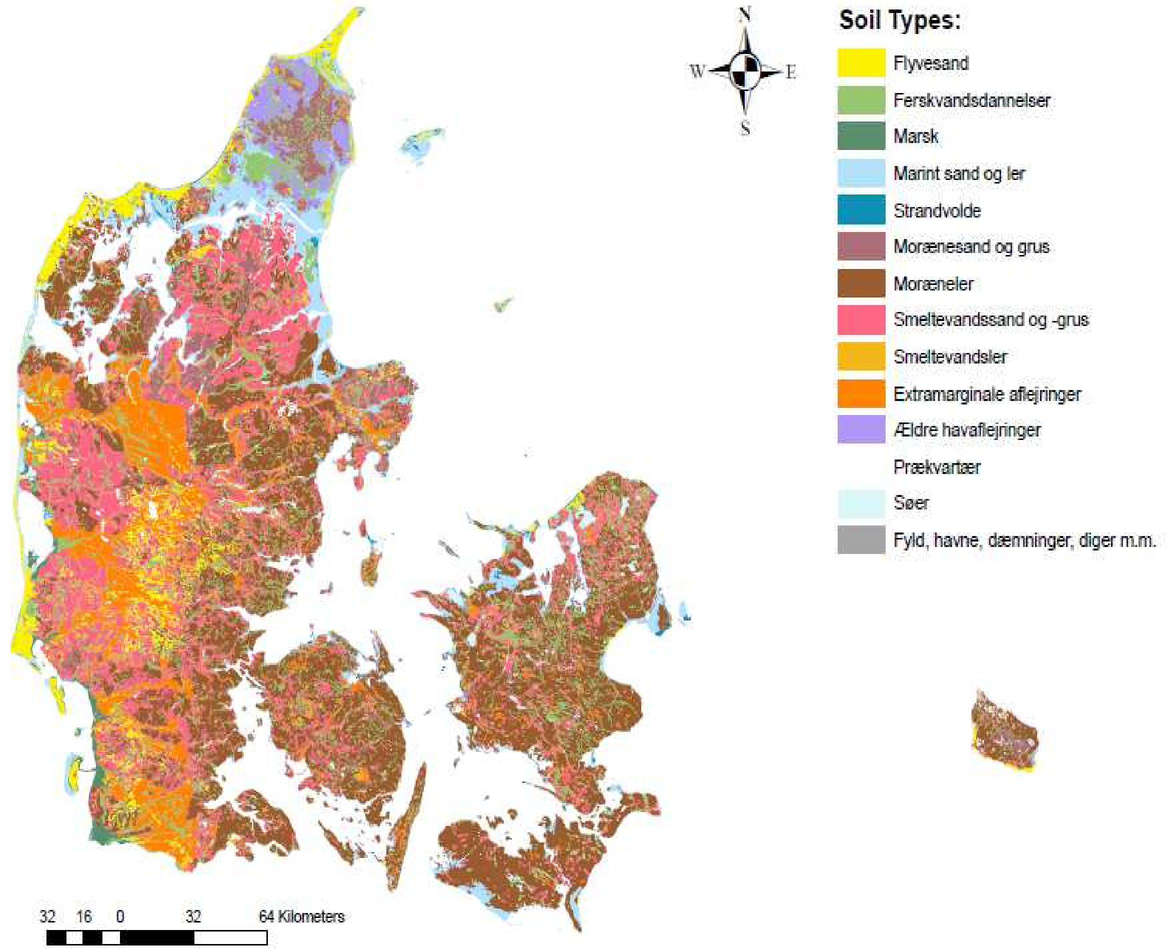


Fig. 27. Soil type classification in Denmark, according to the GEUS_200 map.

Tab. 34. Definition of Danish soil type codes.

	Jord type	**Code**	**Class**	**DJF**		
Postglaciale aflejringer	Flyvesand	ES				
	Saltvandssand	HS				
	Ferskvandsgrus	TG				
	Ferskvandssand	TS				
	Ferskvands snad og grus	TS-TG				
	Saltvandssand	YS	**Sandy**			
Senglaciale aflejringer		S		Jordtype	JB nr.	Teksturdefinition
	Smeltevandsgrus	DG		1	1	Grovsandet jord
	Smeltevandssand	DS		2	2	Finsandet jord
	Morænegrus	MG		3	3	Grov lerblandet sandjord
Glaciale aflejringer	Morænesand	MS			4	Fin lerblandet sandjord
			Loamy Soils	4	5	Grov sandblandet lerjord
	Smeltevandsler	DL			6	Fin sandblandet lerjord
Glaciale aflejringer	Moræneler	ML		5	7	Lerjord

					8	Svær lerjord
				6	9	Meget svær lerjord
					10	siltjord
Postglaciale aflejringer	Ferskvandsgytje Ferskvandstørv	FP FT	**Humic**	7	11	Humus
			Other	8	12	speciel jordtype