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Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem

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We measured on annual basis the magnitude and relative importance of different components of the carbon balance of a boreal Scots pine dominated forest ecosystem. The continuous 10-year-long measurement period of this study and the miscellaneous measurements of the components of the ecosystem carbon balance carried out at the same site are almost unique. The ecosystem was shown to be a carbon sink in all measured years. The average net ecosystem exchange (NEE) estimated with the eddy covariance (EC) method was $^{-}206$ g C m^{-2} a^{-1} and the average annual accumulation of carbon into trees was 242 g C m^{-2} a^{-1}. The above-ground litter production was 186 g C m^{-2} a^{-1} of which 92 g consisted of needles and leaves. The average respiration rates of the soil, canopy and stems were 646, 316 and 62 g C m^{-2} a^{-1}, respectively and the TER deduced from EC measurements was 826 g C m^{-2} a^{-1}. The average rate of the tree and ground vegetation photosynthesis was 982 and 114 g C m^{-2} a^{-1}, respectively. In forest ecosystems the application of biomass equations to measurements of tree dimensions and increment cores can give a reliable and unbiased estimate of carbon accumulation into trees. The chamber based flux measurements are useful in showing short term response to changes in light, temperature and moisture conditions, but the generalization of the results over time and space is difficult.

Introduction

The global carbon balance is a function between a reduction of the atmospheric CO_2 by photosynthesis and oxidation processes releasing CO_2 from previously reduced organic carbohydrate compounds. The life-times of reduced carbon compounds vary significantly. About half are rapidly oxidized in plant metabolic processes and carbon is released back into the atmosphere as CO_2 by autotrophic respiration (e.g. Waring *et al*. 1998). The other half of the assimilates form permanent organic structures that eventually end up in the soil, where microbes oxidise them in decomposition processes and return the CO_2 to atmosphere by heterotrophic respiration. The age of the assimilated carbon stored in the biomass depends on the plant species, varying typically from one to several hundreds of years. The large time-span between the reducing and oxidising processes imply that understanding the dynamics of the carbon balance of an ecosystem requires that both carbon fluxes and changes in carbon storages need to be measured and analysed over long periods. The spatial scale of these measurements can vary from the cell organ to whole ecosystems while the temporal scale involves immediate responses of reducing and oxidising reactions to the environment, the resulting net fluxes varying over seasons and years (*see* Kolari *et al.* 2009) and gradual changes of biomass occurring over several decades.

Carbon sequestration from the atmosphere to forest biomass and the release of carbon dioxide and other greenhouse gases from soil organic matter is one of the key issues in the global carbon balance. It has been estimated, that soil organic matter contains twice the amount of carbon stored in the atmosphere (Kirschbaum 2000). Eurasian forests currently cover around 1.6 billion ha across the continent, making up 41% of the total global forested area (FAO 2001). Approximately, half of the Eurasian forests are located in boreal areas, one fifth in temperate, and one third in subtropical and tropical areas. Both coniferous and broadleaved forests are widely distributed across the entire continent (FAO 2001). The estimated Eurasian forest biomass is 138 Pg dry matter (roughly 70 Pg C) (FAO 1995), being 32% of the global forest biomass. Current estimates of the world's soil carbon pool average 1500 Pg (C). Half of the world's biologically bound carbon is in forest biomes and boreal forests are the largest single terrestrial carbon pool, estimated to contain approximately 15% of the soil C storage world wide (Schlesinger 1977, Post *et al.* 1982, IPPC 2003). On a global scale soils are currently assumed to be carbon sinks (Scholes 1999). However, the factors controlling carbon exchange between forest soil and atmosphere, and the magnitude of the carbon flows in forests utilised by varying methods are still incompletely known and subject to debate (Valentini *et al.* 2000, Trumbore 2006).

In Finland, the estimated forest carbon storages in tree stands are 820 Tg (Liski *et al.* 2006), in mineral soils 921 Tg (Ilvesniemi *et al.* 2002) and in peat soil 5600 Tg (Minkkinen 1999). Annually a forest area of about 145 000 ha is clear-cut and the area of thinnings has been over 300 000 ha (Finnish Forest Research Institute 2007). In 2005, a stem volume of 67 million m^3 was removed in cuttings and the estimated annual growth in the period 1999–2005 was 97 million m^3 a^{-1} (Korhonen *et al.* 2006). The resulting difference of 30 million m^3 corresponds roughly to 0.7 Tg C. In the context of forestry management as a strategy to mitigate atmospheric CO_2 increase, it is important to have accurate data on forest biomass and biomass changes (Ceulemans *et al.* 1999). In areas where forestry operations are intensively carried out the effect of forest management on the carbon cycling is an important issue but so far not very well known (Johnson and Curtis 2001).

In the literature, presumably due to the economical significance of the stem wood, the estimation methods of the amount of stem volume of different tree species are well documented and tested (e.g. Koivisto 1959, Ilvessalo and Ilvessalo 1975, Laasasenaho 1982), but less information is available on the estimation of the quantity of the other tree parts, such as needles, branches and roots (Mälkönen 1974, Hakkila 1979, Marklund 1987, 1988, Vanninen *et al.* 1996, Lehtonen 2005, Repola *et al.* 2007).

In general the annual C fixation in boreal and temperate coniferous forests has been considered to equal to net biomass increment of the trees, if the stand has been undisturbed for a certain time span (e.g. Kolari *et al.* 2004, Schelhaas *et al.* 2004) — with some notable exceptions where the ecosystem is only a weak sink or even a source of CO_2 despite the increase of the tree biomass (Lindroth *et al.* 1998). In transition forests, that is, after management of the stand by harvesting or drainage, the C balance may differ from a naturally growing stand (e.g. Lohila *et al.* 2007).

Measurements where carbon stores and changes in living and dead biomass, as well as all the assimilation and respiration components are measured simultaneously in the same ecosystem, are very rare (Barford *et al.* 2001, Urbanski *et al.* 2007, Gough *et al.* 2008). Such encompassing measurements are valuable, because they contribute greatly in separating the responses of different processes to changes in environmental conditions and to estimate the significance of those processes which are very difficult to measure directly.

In this study, we compare the results of carbon accumulation calculations based on biomass measurements (trees, ground vegetation, litter, soil organic matter) with values obtained from measurements of soil CO_2 efflux, canopy and ground vegetation photosynthesis and EC measurements. We discuss the accuracy and the advantages and disadvantages of different approaches in estimating the annual carbon balance of a given boreal forest ecosystem. The continuous 10-year-long measurement period of this study and the miscellaneous measurements of the components of the ecosystem carbon balance carried out at the same site provide a unique possibility for such comparisons.

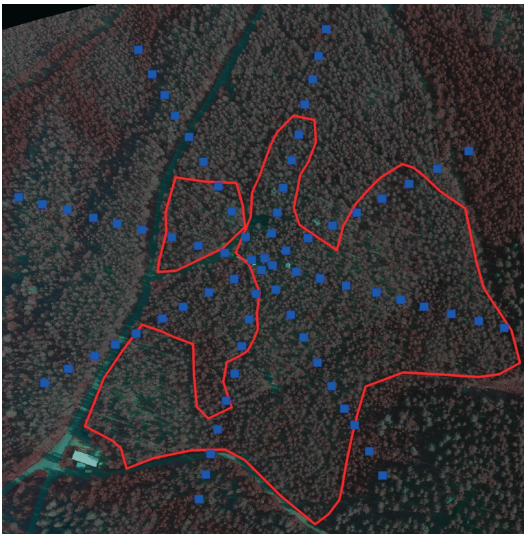

Fig. 1. The aerial photography of the footprint of the eddy covariance mast and the location of the sampling plots. The EC mast locates in the origo. The distance between sample plots was 20 m and the longest distance from mast to sample plot center was 195 m. Areas from where trees were removed in thinning are shown by a read line.

Material and methods

Site

The measurement site at the SMEAR II station is located in southern Finland (61°51´N, 24°17´E, 160–180 m a.s.l.) with the EC mast located at the highest spot in the area (181 m a.s.l.). It is a typical boreal pine dominated coniferous forest (Fig. 1). The area around the EC mast had been regenerated after clear-cutting by prescribed burning and sowing by Scots pine seeds in 1962. Due to the postglacial history, the upland mineral soils in the area are mainly podzols with some bedrock outcrop with almost no topsoil. Some small areas with peat soil are found in the depressions.

Inventory method of tree biomass stores

Sampling design

The aim of the inventory was to estimate the biomass stock variables on circular sample plots with varying radial distances from the EC mast. The variables of interest were the total biomass of the trees and the structural components of the trees (stem, branches, needles and roots). The sampling design was planned so that it allowed biomass calculations both as an arithmetic average of the sample plots and calculations taking into account the varying land area that a single sample plot represented at different distances from the EC mast.

The stand inventory, which was combined with increment core sampling, was done during the autumns of 2001 and 2008. The dimensions of the standing trees (without increment coring) were also measured in 2001 and annually since the year 2003. Systematic plot sampling along radial directions starting from the mast was used. The circular sample plots (100 m^2) were located on 8 (16 in 2001) radials whose central point was the mast. The plot interval was 20 m, and the center of the first plot was located 5 meters from the mast in the N and S radials, 10 m in the E and W radials, 25 m in the NE, SE, SW and NW radials and 45 m in the 8 other radials (Fig. 1). In the winter of 2001–2002 a section of the area was thinned (from 35 plots out of 76 at least one tree was removed) and the total amount of stem volume removed from the area of 4.3 ha was 141 m^3.

Measurements on the plot

From all trees with a diameter > 1 cm at 1.3 m (tally trees) the tree species was recorded and the breast height diameter was measured. Every 7th tally tree was selected as a sample tree whose height was measured and every second sample tree was selected as a growth sample tree (2001 and 2008). From the sample trees, the bark thickness at the inventory time and past diameter increments from increment cores were measured during the last 5- (2001) and 7-year (2008) periods. The annual diameter increments were measured from the increment cores in the laboratory with a tree ring microscope. The height measurement was done with a Vertex hypsometer.

The following tree species were recorded: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver birch (*Betula pendula*), downy birch (*Betula pubescens*), European aspen (*Populus tremula*), willow (*Salix* sp.), common juniper (*Juniperus communis*), mountain ash (*Sorbus aucuparia*), grey alder (*Alnus incana*) and lodgepole pine (*Pinus contorta*). The number and some measured characteristics of the tree population in the footprint area are shown in Table 1.

Calculations

Overview

The results for the concentric circular areas around the EC tower were calculated from the sample plot data. The different target areas for which the values were calculated were 35–195 m from the EC tower with 20-m intervals. The plot sample estimates for the studied variables were calculated from the tally trees by year. Therefore, the diameters, heights and biomasses were estimated for each tally tree for each year in the study period by applying the measured sample tree information and existing models for total biomass and biomass components.

The calculation was made in four phases:

1. Generalization of the sample tree data (diameter and height).
2. Prediction of the total tree biomass and biomass components.
3. Calculation of the plot level variables.
4. Calculation of the variables by area.

Generalization of the sample tree data

The missing diameters and heights were estimated with mixed linear models based on the sample trees. In the models, the random variation was separated into the variation between and within plots. The sample tree variables were estimated for the tally trees with plotwise calibrated models. The parameters of the mixed linear models were estimated and the plotwise random effects were calculated with the Mixed procedure of the SAS statistical package (Littell *et al*. 1996).

The generalization of the sample tree data to the tally trees was done in two phases: (1) estimating the diameter on bark at 1–5(7) years before the inventory (5 preceding years in 2001 and 7 preceding years in 2008), and (2) estimating the height of the tally tree at the time of inventory and 5(7) years before that. The estimations of the diameters on bark at 1–5(7) years before the inventory were made in three phases. First, the diameter without bark at the time of inventory was estimated with a bark model based on diameter on bark (model 3, Appendix 1). Second, the diameter without bark at 1–5(7) years before the inventory were estimated with a diameter increment model that was derived from the increment core measurements (model 5). Finally, the diameter on bark at 1–5(7) years before the inventory was predicted with the bark model as a function of the diameter without bark (model 4) (*see* also Appendix).

A model for the past 5 years height increment (ih5) for all tree species was developed from the 2001 data as a function of the diameter growth:

$$\begin{aligned} \mathrm{ih5} = \exp[&0.62709 - 0.0847\mathrm{sp} \\ &+ 0.10089\ln(\mathrm{id5})] \end{aligned} \tag{1}$$

where id5 is the diameter increment in the past 5 years and sp is a species indicator variable with the value 1 for spruce and 0 for other species. The same equation was used with annual values to calculate the annual height increments.

Prediction of the total tree biomass

The tree biomasses were predicted with the biomass functions where the independent variables were tree species, diameter and height (Marklund 1987, 1988). The total biomass was calculated as a sum of the estimates for stem with bark, living branches including needles, dead branches and stumps together with coarse roots. The models for birch (*Betula pubescens* and *Betula verrucosa*) were used for all deciduous trees. The model set for birch was not complete, because the model for the stumps and coarse roots was lacking and the model for living branches for birch did not include the foliage. The model for pine was used for the stumps and coarse roots but the foliage of the deciduous trees are missing from the final results of the biomass increment calculations.

Calculation of the plot level variables

The plot-level sum variables were calculated directly as a sum of the values of the individual trees. The plot-level values were then transformed to values per hectare by dividing the plotwise sums by the plot area. The annual changes of the plotwise variables were simply the differences between the values of two successive years. The data based on annual tree dimension measurements was calculated with the same biomass equations as the data based on the increment cores.

Calculation of the variables by area

The estimates of the variables by the concentric areas with 20 m intervals (range = 35–195 m) were made using estimators for random sampling. The sample plots were weighed by the area they represented or as an arithmetic average of the sample plot results.

Ground vegetation biomass and biomass accumulation

In the years 2003–2006 and 2008, the average biomass of the ground vegetation at the study site was estimated by collecting samples of the aboveground plant parts. The plots were the same as for the tree biomass sampling in 2008, added with two plots 5 m NE and SE from the mast (Fig. 1). The ground vegetation biomass samples were collected in the end of July and beginning of August. The sample size was 0.053 m^2 (0.033 m^2 in 2006). Each sample was separated into different species, and each species

Table 1. The number of different tree species and the average stand characteristics of the trees growing in year 2006 in the 200 m radius area around the EC mast. The data is shown separately for pine, spruce and broadleaved species, and also separately for trees with the diameter at breast height above and below 5 cm. The crown height of the spruces below 5 cm in diameter was not measured.

Tree size	Tree species	Number of trees ha^{-1}	Diameter at breast height (cm)	Stem basal area (m^2 ha^{-1})	Height (m)	Crown height (m)
All trees	Pine	959	14.1	18.0	15.5	8.7
	Spruce	1107	3.9	3.3	6.8	2.8
	Broadleaved	3574	1.8	2.9	5.5	5.8
	All species	5640	4.3	24.3	7.5	5.7
Trees with DBH ≥ 5 cm	Pine	845	15.7	18.0	15.8	8.9
	Spruce	234	11.0	3.0	12.3	2.8
	Broadleaved	293	9.0	2.2	14.0	6.0
	All species	1373	13.4	23.2	14.8	7.2
Trees with DBH < 5 cm	Pine	114	2.7	0.1	7.6	4.4
	Spruce	874	2.0	0.4	2.3	
	Broadleaved	3281	1.2	0.6	3.0	1.9
	All species	4268	1.4	1.1	3.0	

into leaves and stem. From the mosses, the green parts were separated from the shoots. Finally, the different segments were weighed after drying in 60 °C for 24 hours.

Humus and root sampling

In 2003, the amount of organic matter in the humus layer was measured in an inventory from the same radial plots that were used for the tree inventories in 2008 (Fig. 1). One sample per plot was collected. The roots found in these 0.053 m^2 samples were separated and weighed. A more detailed analysis of the amount of different species and of the depth gradient of roots and carbon in mineral soil was made with a subset of samples ($n = 26$) taken with a steel auger (diameter = 50 mm) to the depth of 50 cm. The roots were manually separated and weighed for living parts of Scots pine, Norway spruce, broadleaved trees, dwarf shrubs and herbs.

Litterfall

The amount of the aboveground litterfall was measured every month from 20 litterfall collectors, which were randomly distributed on the two mini-catchments of the SMEAR II station (40 × 40 m area, 50 m NE from the tower). The litterfall collectors were positioned 60 cm above the ground, collecting the litter originating from the trees but not from the ground vegetation. The samples were collected once a month, separated for needles and leaves and other litter, dried in 60 °C for 24 h and weighed. An annual litterfall was calculated by summing up the monthly values. The amount of branch litter was measured once a year from 50 × 100 cm frames lying on the ground. Root litter was estimated from the root and needle biomass measurements and ground vegetation litter from the ground vegetation biomass measurements by assuming the average life time of the measured plant organ.

Outflow

The amount of runoff was measured from two weirs on the two mini-catchments of the SMEAR II station and the dissolved organic carbon of the samples was measured with a TOC analyzer (Shimadzu TOC 5000, Japan).

Ecosystem carbon exchange

On the ecosystem level, NEE was determined by means of the eddy covariance method (EC). In this technique, the instantaneous vertical wind velocity w and a scalar c (here the mixing ratio of CO_2) are measured simultaneously about 10 meters above the forest canopy, and the flux F is calculated as the 30-minute average of the product of the instantaneous fluctuations (w', c') around the mean values: $F = \rho\overline{w'c'}$, where ρ is the density of the dry air. This measurement gives an estimate of the net CO_2 exchange of the whole ecosystem. The instrumentation consists of a 3D ultrasonic anemometer, sampling tubing and an infrared gas analyser (details in Vesala *et al.* 2005). The measuring height of the fluxes was 23 m except from April 1998 until June 2000 when the fluxes were measured at 46 m.

The half-hourly averaged NEE were filtered using threshold values for friction velocity or atmospheric stability (Markkanen *et al.* 2001) and corrected for changes in storage of CO_2 below the measuring height. The NEE was partitioned into TER and GPP as documented in Kolari *et al.* (2009). The half-hourly TER was modelled from nighttime NEE measurements as an Arrhenius type function (Lloyd and Taylor 1994) of the soil organic layer temperature. The temperature dependence of the night time TER was applied to daytime, and the half-hourly daytime GPP was computed by subtracting the estimated TER from the measured NEE. In case of missing or rejected NEE, the half-hourly GPP was calculated from a saturating light response parameterised with the accepted NEE data. The temperature sensitivity of the TER and the curvature of the photosynthetic light response were estimated over a 2-month period during the summer, fixed parameter values were then applied for the whole year. The base level of the TER as well as light-saturated GPP were estimated daily in a moving time window of 11 days.

Photosynthesis and respiration

The photosynthesis and respiration in the stand were determined by integrating chamber-based component CO_2 fluxes of 3–4 chambers over the stand. The flux measurements and modelling as well as the spatial and temporal integration (half hour steps) of the fluxes have been documented in detail in Kolari *et al*. (2009). Here we will give only a brief outline of the methods used.

The photosynthetic production of the coniferous trees was calculated with the stand photosynthesis model SPP (Mäkelä *et al*. 2006). The model consists of a light-attenuation model from Oker-Blom *et al*. (1989) coupled with a leaf-level photosynthesis model (Hari *et al*. 1986, Mäkelä *et al*. 2004) and a model of Duursma *et al*. (2008). The photosynthesis model was originally parameterized with automated shoot chamber data (Kolari *et al*. 2007).

The ground vegetation photosynthesis was measured separately for blueberry (*Vaccinium myrtillus*), lingonberry (*Vaccinum vitis-idea*), smallreed (*Calamagrostis epigejos*) and heather (*Calluna vulgaris*) plants, and patches of feather mosses (*Pleurozium schreberi* and *Dicranum polysetum*) in two-week intervals with an opaque, manually operated closed chamber. The 4–5 light intensities were created by covering the chamber with one or more layers of nettic fabric. One measurement ended in a dark measurement, when an aluminium sheet was placed to cover the chamber and hinder photosynthesis. In the end of the growing season the measured above ground parts of the plants were collected, dried and weighed. The measured ground vegetation species composition, species-specific photosynthesis rates and continuous temperature and light measurements were used for up-scaling the annual amount of photosynthesis in the area. The below-canopy light intensity was estimated with the same model that was used for shoot light attenuation. The details of the measurements and up-scaling are described in Kolari *et al*. (2006).

Respiration of the ground vegetation was embedded in the CO_2 efflux from the soil and not estimated separately.

The stem respiration was measured with chambers connected to an automatic gas exchange system of the SMEAR II station; two chambers were connected to the measuring system at a time. The measurements and the estimation of the annual respiration using the information of the size of the trees in the stand are described in detail in Kolari *et al*. (2009).

The soil respiration (R_s) was measured continuously with 2–3 automated transparent chambers (d and h = 20 cm). In the first years until the year 2000, the vegetation was removed from the chambers, later the ground vegetation in the chamber was left untouched but the amount of plants was lower than in the area in general. Since 2004, the places of the soil chambers have been changed. The chamber has a lid that closes automatically once an hour for the measurement period of 70 s. A continuous air flow was directed through the chamber to the automatic gas exchange system of the SMEAR II station. The technical details of the chambers are described in Pumpanen *et al*. (2001). The determination of the calibration coefficient of the chamber in controlled CO_2 flux conditions (= 0.93) is documented in Pumpanen *et al*. (2004). Nighttime CO_2 effluxes from the chambers were used to parameterize the temperature response of R_s. The mean of the temperatures measured in the organic layer and in the mineral soil surface (A-horizon) was used as the explanatory factor in the model used to calculate the daytime soil respiration. Between April and November, the proportion of direct respiration measurements was ca. 40%. To take into account the seasonal variation not directly related to temperature, the response function was re-scaled daily by estimating the base level of respiration in a moving time window of three days while keeping the temperature sensitivity constant. The soil CO_2 efflux was estimated also by integrating the results of the direct chamber based measurements. This value includes also the effect of daytime ground vegetation photosynthesis resembling a value of the NEE at ground level. The annual CO_2 efflux integrated from the automated chambers was scaled by applying the information of the spatial variability of the CO_2 efflux obtained from the measurements conducted on at least 14 collars several times a year. The scaling factor varied annually between 0.82 and 0.97. In winter, the operation of the chamber was reduced, and a temperature response or a constant flux was applied.

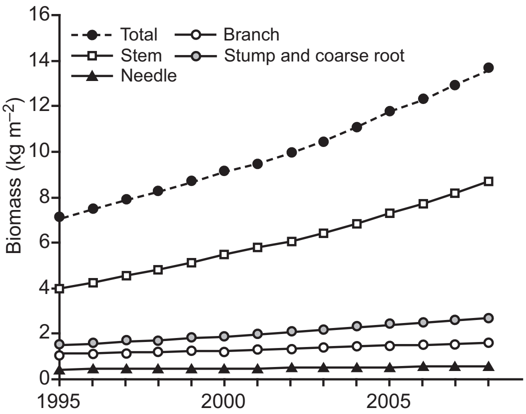

Fig. 2. The average biomass of different tree compartments (195 m radius area). The values are expressed in biomass units, an estimate of the carbon content of the biomass can be obtained by multiplying the biomass value by a factor of 0.5.

Results

Biomass accumulation in the trees

Measurements based on sample trees and increment cores

In 2008, the total tree biomass in the 200-m radius area was 13.7 kg m^{-2} corresponding to 6.8 kg C m^{-2} (Table 2). Since the establishment of the SMEAR II station in 1995 the biomass stored in the trees has almost doubled, corresponding to a carbon sequestration of 3.3 kg C m^{-2}, which gives an annual average of 243 g C m^{-2} (Fig. 2, Table 2). The biomass of the trees increased continuously during the measurement period except for the year of thinning (thinning between December 2001 and March 2002).

The estimated amount of the total biomass and biomass accumulation differs in areas with different distance from the EC mast. The most obvious difference is that the increase is smallest on the plots closest to the EC mast. The mast is on the highest spot of the study area and, because of the glacial history, the top of the hill is covered by a thin layer of soil or even open bedrock without any soil on it which causes low site productivity. Contrary, when the biomass accumulation is calculated separately for each 20-m-wide circular area around the mast, the most distant sample plots have the highest biomass accumulation.

Due to the variation within the sample plots, the estimated biomass accumulation depends to some extent on the method of weighing the area a single sample plot represents. When the calculation was made along an increasing radius, the area represented by a single sample plot increases, and the biomass of the most distant sample plots gets higher weight. If the value of each sample plot is used without radial weight, then the sample plots near the mast with smaller

Table 2. Annual total tree biomass (kg m^{-2}) calculated separately for sample plots representing different radius around the mast.

	35 m	55 m	75 m	95 m	115 m	135 m	155 m	175 m	195 m
2008	11.3	12.7	13.6	13.9	14.5	13.5	13.5	13.8	13.7
2007	10.8	12.2	13.1	13.4	13.9	12.9	13.0	13.2	13.1
2006	10.3	11.7	12.5	12.8	13.3	12.4	12.4	12.6	12.5
2005	9.9	11.2	12.0	12.3	12.8	11.9	11.9	12.1	11.9
2004	9.4	10.7	11.4	11.7	12.2	11.3	11.4	11.5	11.4
2003	8.9	10.2	10.9	11.1	11.6	10.7	10.8	10.9	10.8
2002	8.5	9.7	10.4	10.7	11.1	10.3	10.4	10.5	10.3
2001	8.6	10.1	9.4	11.1	11.0	10.3	9.8	9.6	9.5
2000	8.2	9.7	9.0	10.6	10.5	9.8	9.3	9.2	9.1
1999	7.8	9.1	8.5	10.0	9.9	9.3	8.9	8.7	8.6
1998	7.4	8.7	8.0	9.5	9.5	8.9	8.4	8.3	8.2
1997	7.0	8.2	7.7	9.1	9.0	8.5	8.0	7.9	7.8
1996	6.6	7.8	7.2	8.6	8.5	8.0	7.6	7.4	7.4
1995	6.2	7.3	6.8	8.1	8.1	7.6	7.2	7.0	7.0

trees will have a stronger impact on the biomass estimate. The annual differences between the methods at different radiuses were in the range of 1–17 g C m^{-2} a^{-1}. The variation between the tree biomass of every 20-m belts around the EC mast was higher (Table 2).

Within radiuses below 150 m, the decrease in the tree biomass caused by the thinning can be seen after the year 2001, but the effect varies depending on the intensity of the thinning and the proportion of the thinned sample plots of all measured plots (Table 2). When the radius of the area was 150 m or more, the effect of thinning on the average total tree biomass was negligible. The biomass calculations were made using biomass functions, including an allocation ratio between the tree compartments, so it is obvious that also the biomass increase of all tree compartments shows a similar trend as the total biomass (Fig. 2).

The annual biomass accumulation in the 1990s had been around 200 g C m^{-2} a^{-1}, and increased to 300 g C m^{-2} a^{-1} in 2008. The stem growth was the major contributor (> 70%) to this accumulation. The variation in the accumulation rate between years is typically in the range of ±25 g C m^{-2} a^{-1} (Fig. 3). A similar spatial pattern as for the total biomass in the areas with different radiuses can also be seen in the annual biomass accumulation. During the measurement period, the growing stock of the trees increased, and the annual growth of the trees also increased. The average age (45 yrs) and tree size represented the stage in the life-cycle of a stand when the annual growth is at its highest.

The larger the sampling area (increase in the number of sample plots) the smaller is the relative sampling error. As the radius of the area increased from 35 m to 195 m and the number of sample plots increased from 12 to 76 the relative error decreased from ca. 15% to ca. 5%. Especially on the sample plots in the immediate vicinity of the mast the relative sampling error is higher, which is partially also explained by the smaller number of sample plots included in the analysis. The relative sampling errors of the annual growth were in the same range or even smaller than the sampling errors of the total biomass except in the immediate vicinity of the mast.

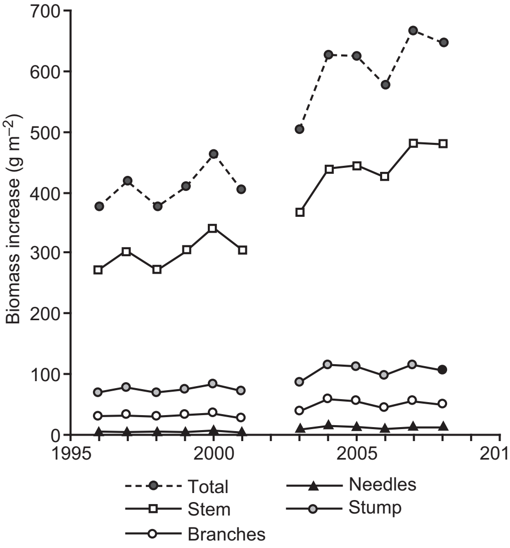

Fig. 3. The annual average biomass increase of different tree compartments during the measurement period. The values are averages of all sample plots. The values of the compartment growth for the year 2002 are not shown due to thinning carried out that year between two consecutive inventories.

The biomass estimations based on annual diameter and height measurements

The biomass of the different tree compartments of pine, spruce and broadleaved species was calculated also using the annual diameter and height measurements. The total biomass and the increase in biomasses over the period 2002–2008 were in the same range as the values obtained from the calculations based on the increment cores. However, the annual biomass accumulation based on the difference between the measurement results of two successive years was in some cases almost zero and between some other years almost twice as high as the average annual growth. It can be concluded that for the estimation of annual biomass accumulation the successive measurements of tree dimensions did not give reliable values. The proportion of pine of the total stem biomass was ca. 75% and spruce and other tree species both amounted to ca. 12% each. The needle or leaf (= foliage) biomass was divided between tree species in a very different manner since the proportion of pine needles was 50%, spruce needles 30% and leaves 20% (Table 3, *see* also Table 1 for other stand characteristics).

Ground vegetation

The most common vascular plant species growing on the measured plots were lingonberry (*Vaccinium vitis-idaea)* and blueberry (*Vaccinium myrtillus*). Other common vascular species in the order of decreasing abundance were *Deschampsia flexuosa*, *Trientalis europaea*, *Maianthemum bifolium*, *Linnea borealis*, *Calluna vulgaris*, *Calamagrostis epigejos*, *Luzula pilosa* and *Oxalis acetosella*. The most frequent mosses were *Pleurozium schreberi* and *Dicranum polysetum*. Other common mosses were *Polytrichum* sp., *Hylocomium splendens* and *Sphagnum* sp. The average dry mass of the above-ground vegetation was 126 g m^{-2} and the annual average above ground biomass estimates were 133, 121, 143 and 144 g m^{-2} in the years 2003, 2005, 2006 and 2008 respectively (Fig. 4). In 2004, presumably due to severe spring frosts, the biomass of the ground vegetation was smallest with an average of only 94 g m^{-2}. The biomass of grasses, herbs and mosses had an increasing trend from 2004 to 2008, showing a recovery from the frost, but otherwise it is not possible to determine whether there was an annual accumulation of the total ground vegetation biomass. Some lichens (mainly *Cladonia* sp.) grow on bedrock outcrops but they were not analysed as a part of the ground vegetation. The average dry mass of the lichens is around 8 g m^{-2}.

Carbon in roots and soil

The total average fine-root biomass in the humus and mineral soil layers was 476 g m^{-2}. The major proportion of the roots was pine roots, which agrees well with the proportion of this species of the above ground biomass (Table 4).

Table 3. The biomass of different compartments (kg m^{-2}) of pine, spruce and broadleaved trees calculated from the annual diameter and height measurements of the sample plots. The root category includes stumps and coarse roots but not fine roots.

		Stem	Branch	Needles	Roots	Total
2008	pine	6.17	1.25	0.32	1.95	9.68
	spruce	1.09	0.53	0.20	0.43	2.26
	broadleaved	0.95	0.22	0.09	0.20	1.46
	total	8.21	2.00	0.61	2.58	13.40
2006	pine	5.72	1.17	0.30	1.80	8.99
	spruce	0.95	0.47	0.18	0.38	1.98
	broadleaved	0.93	0.22	0.10	0.20	1.45
	total	7.60	1.87	0.58	2.38	12.42
2005	pine	5.25	1.13	0.29	1.69	8.36
	spruce	0.87	0.44	0.17	0.35	1.82
	broadleaved	0.85	0.21	0.09	0.19	1.34
	total	6.96	1.78	0.55	2.23	11.52
2004	pine	5.16	1.14	0.29	1.67	8.26
	spruce	0.85	0.48	0.19	0.37	1.89
	broadleaved	0.86	0.21	0.10	0.19	1.34
	total	6.86	1.83	0.58	2.22	11.49
2003	pine	4.68	1.08	0.28	1.54	7.58
	spruce	0.82	0.42	0.16	0.32	1.72
	broadleaved	0.67	0.11	0.05	0.09	0.92
	total	6.17	1.60	0.49	1.95	10.21
2001	pine	4.25	1.09	0.30	1.44	7.08
	spruce	0.77	0.42	0.16	0.33	1.68
	broadleaved	0.60	0.16	0.06	0.14	0.97
	total	5.63	1.67	0.52	1.92	9.73

The average fine root biomass measured from 69 humus samples was 259 g m^{-2}.

The average amount of carbon in the humus layer was 1.68 kg C m^{-2}. The total amount of soil carbon to the depth of 50 cm, measured from a part of the area, was 6.56 kg m^{-2}. There was no time series available to determine any possible change in the amount of below-ground plant organs or the amount of carbon in the humus layer.

Litterfall

The annual average above-ground litterfall was measured in the near vicinity of the mast, but not representatively from the measured 200 m radius area. Excluding the year of thinning, the annual amount of canopy litter varied between 115 and 170 g C m^{-2}. The range in the branch litter that was collected separately was between 13 and 46 g C m^{-2} (Table 5). Some of the smallest branches could be analysed using both collection methods causing a small overlap in the results. The proportion of needles of the canopy litter was high, 55%–75% of the annual amount. More than half of the litter was shed in September–October. In those months the variation between the collectors was also at its lowest (standard deviation was 25% of the average) emphasizing the importance of autumn measurements for the accuracy of the annual litterfall estimates.

In 2003–2007, the biomass of blueberry leaves and grasses, lingonberry leaves and green parts of mossess varied between 12–18 g m^{-2}, 21–30 g m^{-2} and 34–53 g m^{-2}, respectively. Grasses and blueberry shed all their leaves annually, the average age of lingonberry leaves is three years and the senescence of mosses varies, but in this study an average turnover rate of 0.20 was used. Based on these assumptions, the annual litterfall of the ground vegetation varied between 15–20 g C m^{-2} which is in the range of 20% of the litter originating from the trees.

The amount of the annual root or other below-ground organ litter could not be measured.

Outflow

The annual average outflow from the catchment located within the measured area was 193 l m^{-2}. The average DOC concentration was 4 mg l^{-1} which gives an annual outflow of 0.8 g C m^{-2} as DOC. In a headwater ecosystem without large peaty areas the influence of the outflow on the total carbon balance is negligible.

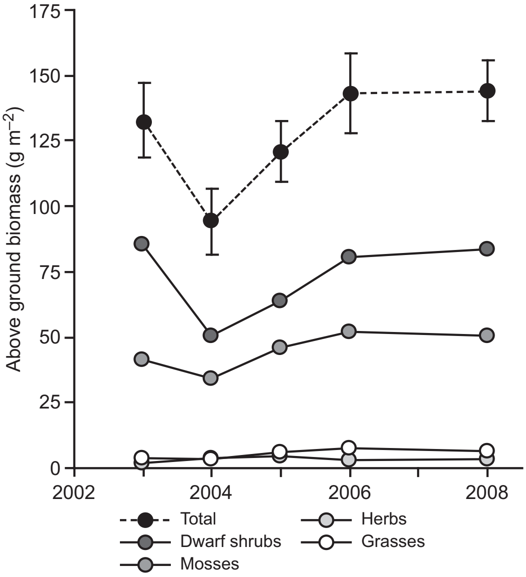

Fig. 4. Above ground biomass of different species groups and total biomass of ground vegetation.

Respiration and photosynthesis

The average annual soil respiration was 646 g C m^{-2} and it varied between 537 and 777 g C m^{-2}. Soil respiration is an important component of the annual carbon balance of this ecosystem because its proportion in the sum of all

Table 4. The biomass of living fine roots in the soil profiles.

	Biomass (g m^{-2})
Birch	6
Other broadleaves	58
Spruce	4
Pine	299
Dwarf shrubs	33
Herbs	13
Other	62
Total	476

respiration components varied between 55% and 70% (Table 6).

The lowest respiration values were obtained during the dry growing seasons of 2002 and 2006. The effect of the litter input from the thinnings could not be observed in the soil respiration or the TER. The uncertainty in the estimation of the soil respiration is large. The amount of soil respiration is sensitive both to the estimation of the wintertime CO_2 efflux and to the way in which the spatial variation is taken into account. On an annual basis approximately 100 g C m^{-2} a^{-1} higher effluxes are obtained, if the fluxes are not scaled for spatial variability with the manual chamber data and the wintertime measurements are rejected and replaced with values based on the regression between CO_2 efflux and soil temperature in late autumn.

If the estimation of the CO_2 efflux is based on interpolation between successive direct measurements, in the years when the ground vegetation was removed (1998–1999) the CO_2 efflux rate was 520 g C m^{-2} a^{-1}. Between the years 2001 and 2005 the efflux rate was 605 g C m^{-2} a^{-1}

Table 5. The annual average amount of branch litter at the ground level (*n* = 20) and needle, twig and cone litter at the height of 60 cm (*n* = 20) and the total above-ground litter. The proportion of needles is calculated from the amount of the canopy litter. n.a. = data not available.

	Branches (g C m^{-2} a^{-1})	Canopy litter (g C m^{-2} a^{-1})	Above-ground litter (g C m^{-2} a^{-1})	Proportion of needles (%)
1997	26.2	115.5	141.7	n.a.
1998	13.4	135.3	148.7	n.a.
1999	37.8	166.1	203.9	n.a.
2000	44.6	145.4	190.0	n.a.
2001	14.2	169.8	184.0	74.5
2002	34.1	268.5	302.6	n.a.
2003	45.6	148.7	194.3	55.6
2004	29.2	113.7	142.9	59.4
2005	31.8	166.4	198.2	57.9
2006	45.6	144.3	189.9	64.8
2007	27.7	119.9	147.6	45.5
2008	n.a.	149.8	149.8	62.5
Average	31.8	154.0	185.8	60.0
SD	11.4	43.0	45.7	8.9

Table 6. The amount of annual GPP, TER, soil, shoot and stem respiration, soil CO_2 efflux and tree and ground vegetation photosynthesis (g C m^{-2} a^{-1}) of the studied ecosystem. GPP and TER are based on EC measurements, respiration and photosynthesis results are based on chamber measurements. Soil CO_2 efflux is the direct result of the chamber measurements including the effect of the ground vegetation photosynthesis. n.a. = data not available.

Year	GPP	TER	Soil respiration	Soil efflux	Shoot respiration	Stem respiration	Tree photosynthesis	Ground veg. photosynthesis
1997	999	777	n.a.	n.a.	335	n.a.	972	n.a.
1998	1004	761	737	590	282	n.a.	905	n.a.
1999	952	815	627	450	337	n.a.	1043	n.a.
2000	1094	898	n.a.	n.a.	315	n.a.	1040	n.a.
2001	991	806	777	651	318	n.a.	954	90
2002	1084	850	602	517	302	67	1025	123
2003	974	833	634	621	300	62	934	108
2004	1068	836	619	599	279	60	950	95
2005	1073	847	637	637	316	64	977	125
2006	1003	801	537	n.a.	368	57	997	135
2007	1104	857	n.a.	n.a.	326	n.a.	1000	125
Average	1031	826	646	581	316	62	982	114

(the total average being 581). The vegetation inside the automatic flux chambers was not as dense as the vegetation in the area in general, and presumably the effect of ground vegetation photosynthesis on the measured soil CO_2-efflux was lower than the average photosynthesis rate estimated in the ground vegetation photosynthesis measurements.

In addition to the soil respiration, the shoot respiration was also substantial, in the order of 300 g C m^{-2} a^{-1}. The estimated amount of the annual average stem respiration was 65 g C m^{-2} a^{-1}.

The annual net photosynthesis of the trees varied between 905 and 1043 g C m^{-2}. The annual average photosynthesis of ground vegetation was 114 g C m^{-2}. The annual variation in photosynthetic production of the ground vegetation depends mostly on the photosynthesizing leaf biomass and light but also on the temperature history. Due to the increase in needle and leaf biomass of the trees, less radiation reaches the ground level. However, the photosynthetic production of the ground vegetation was higher in the three last measured years, being highest in 2006 (135 g C m^{-2} a^{-1}) and lowest in 2001 (90 g C m^{-2} a^{-1}).

NEE and biomass accumulation of the ecosystem

In between the years 1997 and 2007, the annual average GPP was 1031 g C m^{-2} and it varied between 952 and 1104 g C m^{-2}. The annual average TER was 826 g C m^{-2} and it varied between 761 and 898 g C m^{-2}. The annual average NEE (EC) was $^{-}$206 g C m^{-2} and it varied between $^{-}$137 and $^{-}$247 g C m^{-2}. If only the trees within 35 m radius were taken into account the average annual biomass accumulation into the trees was 217 g C m^{-2} and varied between 183 and 255 g C m^{-2}. If all trees from the 200m radius were included the average tree biomass accumulation was 242 g C m^{-2} and between 188 and 292 g C m^{-2}. The carbon accumulation into tree biomass was on an average 36 g C m^{-2} higher than the $^{-}$NEE (Fig. 5). The year 1998 was the only year when the $^{-}$NEE exceeded carbon accumulation to biomass. In the last four years, if the carbon accumulation was calculated for trees growing within 35 m of the EC mast, the values of both measurements were almost equal. If the biomass accumulation of all the trees in the 200-m radius were taken into account the difference between biomass and EC measurements increased during the last measured years.

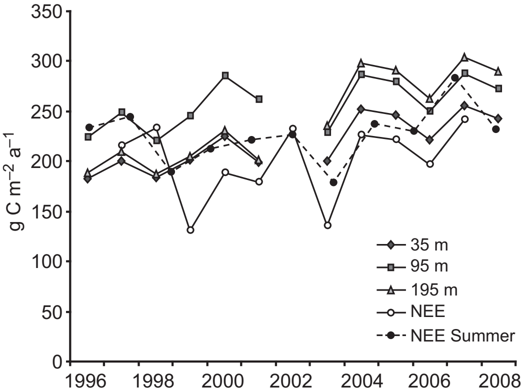

Fig. 5. NEE and carbon accumulation into tree biomass in within 35 m, 95 m and 195 m radius areas during 1997–2007. NEE is presented as its absolute value and for both the period when the main part of tree and ground vegetation growth occurs (May to July) and over the whole year.

When the biomass accumulation was compared against the $^{-}$NEE of the stem growth period from May to July, the difference between the measurements was slightly lower than in calculations over the whole year.

Discussion

Evaluation of the reliability of the tree biomass results

Measurement errors

The evaluation of the measurement errors is based mainly on the short review in the article by Ojansuu (1993). The standard deviations of the random measurement errors of the diameter (0.3 cm), height (3%), bark thickness (0.4 cm) and diameter growth measurements (5%) are small and have no significant influence on the growing stock estimates of the whole area. No significant systematic errors have been reported for those variables. We found no reports on the accuracy of the method of height increment in Finnish conditions where the height increment is determined as the difference between two height measurements. If no systematic errors occur, the measurement errors have a minimal effect on the results of the successive years on the whole area.

Reliability of the generalization of diameter and height information

The tree diameter in the years before the inventory and all tree heights had been estimated with mixed models which had been calibrated to each stand with the aid of the sample tree data. The predictions are only marginally unbiased because the calibrated predictions for each plot are reduced towards the fixed prediction. This affects the estimates by area of the variables which have a nonlinear relationship with the predicted tree diameters or heights (e.g. the biomass). Because of the high number of tally trees, the random errors of the predictions have only a minimal effect on the results. The average height increment is assumed to be similar in relation to the diameter increment as it was five years earlier. This can lead to a minor over-prediction for values of 2002–2008 because of the changing stem form.

Biomass predictions

The tree biomasses have been predicted with existing models based on independent data sets. The statistical parameters of the models describe their reliability in modelling the data. The relative standard error of the total tree biomass can be approximated as a weighed average of the corresponding errors of the biomass compartments (Table 7). The weights are the average proportions of the predicted biomass components from the total biomass (stem is 64%, living branches are 13%, dead branches are 2% and the stump-root system 21%). This means that the standard error of the total tree biomass for pine and birch is about 28% and for spruce about 25%. Marklund (1987) reported that the residual variation within stands is more than four times greater than the between stand variation. Because of that, with an increase in the number of trees in a stand follows an actual decrease of the total standard error of the average biomass estimate. It can be approximated that the standard error of the total biomass estimate for the whole area is below 10%.

Table 7. Standard errors of the used models. The standard errors in the logarithmic scale can be taken as approximations of relative errors in the arithmetic scale.

Dependent variable	Pine	Spruce	Birch
ln(Stem with bark)	0.20	0.17	0.20
ln(Living branches)	0.46	0.37	0.53
ln(Dead branches)	0.86	1.70	1.16
ln(Stump–root system)	0.36	0.34	

The incomplete model set for birch causes errors in the calculations based on increment cores. The foliage compartment of the deciduous trees is missing in Marklund's biomass functions used, which leads to an underestimation of the total biomass. The underestimation caused by the lack of leaves of the deciduous tree functions can be approximated with the proportion of leaf biomass from the total biomass and the proportion of deciduous trees from the total volume. The relative proportion of leaves was assumed to be 5%, and the stem volume of the deciduous trees was 9.4% in the area with the largest radius (195 m) and decreased to 4.5% in the area where the radius was 55 m. In the vicinity of the mast, the deciduous tree volume was 1.5%. Presumably the underestimation due the lack of leaves in the deciduous tree biomass functions may be under 1%. The effect of the use of the pine model to predict the biomass of the stump–root system is difficult to assess.

Estimates of the biomass changes are based on the assumption that it is possible to describe the temporal change in the trees with the cross-sectional biomass models. This assumption can be done under two conditions: (1) new biomass is formed in an allometric relation to the tree dimensions, and (2) litter is formed in an allometric relation to the tree dimensions. The first condition may be true. The second condition may be true for a longer period, but the litterfall can vary from year to year.

Sampling error

The relative sampling error for all static variables and biomass changes diminishes rapidly to the radial 95 m and is about 5% with longer radii. Estimators for the random sampling have been used, though the sampling was systematic. The estimates are unbiased, but the estimated sampling errors are over-predictions because systematic sampling is always more effective than random sampling when the measured variables are autocorrelated (Matérn 1960).

Summary of the reliability

The reliability of the biomass results by areas is affected by random and systematic components. It is apparent that random errors caused by measurement, generalization of sample tree information, prediction of total biomass and sampling are independent. We approximate the error variance for the areal estimates caused by random factors with the sum of the prediction variance and sampling variance. The relative standard errors of the biomass models were 0.1 and they were expected to be independent of the radius. The standard error of sampling was a function of the radius and it decreased from 0.131 in the smallest radius to 0.044 in the largest radius. The corresponding change in the total standard error was from 0.164 to 0.109. The effects of measurement errors and generalization errors have not been taken into account because it can be assumed that the overestimate of the sampling error has a greater effect on the total variance.

The retrospective estimation of the carbon accumulation into tree biomass using tree diameter and height measurements, increment cores and biomass equations is relatively easy to carry out. The reliability of the estimate can be measured and long periods of time can be covered. Based on the comparison of the results of annual measurements of tree dimensions and results based on single measurement with increment core samples, it seems that there is no need for the annual tree dimension measurements. On the contrary, the results are more reliable, if increment cores are used instead of successive tree dimension measurements. When this method is applied in general, it has to be taken into account that many forests are subject to thinnings, where a proportion of stems are removed. In our case we measured first carbon accumulation into the tree population existing prior the thinning, and further into the tree population growing in the footprint after thinning. Due to the different tree populations in two samplings, the C accumulation during the year of thinning (2002) could not be determined reliably. It is interesting that already in next season (2003) the accumulation of carbon to the remaining trees was on similar level as it had been before thinning, suggesting that the remaining trees could utilize the released space for their growth. It can be also assumed that the observed increase in annual biomass accumulation in the last measured years is at least partially related to the thinning effect.

Evaluation of the reliability of the other biomass measurements

The measurements of the ground vegetation biomass, root biomass and soil carbon stores are based on samples collected from the same sample plots as tree measurements were done or from the two small catchments in the vicinity of the EC mast. The spatial variation in all these measured components was high. Especially the separation of roots from humus and mineral soil is a very tedious task, thus reducing the number of root biomass samples substantially. The shift between humus and mineral soil is sometimes difficult to determine, also the definition between above- and below-ground plant organs is difficult especially with dwarf shrubs.

The ground vegetation samples were collected in late July and the beginning of August representing the maximum annual biomass. The estimation of the annual accumulation in the ground vegetation biomass was difficult due to a large variation between the samples and small differences in the annual values. In 2002 and in autumn 2003 there were severe summer droughts which may have decreased the production of the ground vegetation and therefore also the growth in the following year may have been smaller than normally. In May 2004, severe night frosts occurred after a warm start of the growing season damaging the growing tissues and causing the death of a part of the new blueberry shoots. This frost episode can explain the low biomass in 2004.

The litterfall collection was done with 21 (later 20) samplers installed within the two small catchments near the EC mast. The number of samplers as such was sufficient to give a good estimate of the amount of litterfall and its variation, but the values did not represent the whole measured area. The amount of the ground vegetation litter and root litter could not be measured and was estimated from the biomass of the annual parts of the plants and average senescence rates. The amount of plants that senescence annually gave a rough estimate of the range of litterfall of the ground vegetation.

Evaluation of the reliability of the flux measurements

The fraction of soil, stem or needle surface area covered by chambers is very small as compared with the total soil, needle or stem surface. The spatial variation of the soil CO_2-efflux was high, and within one day the efflux rate followed the variation in soil surface temperature. It can be assumed that the diurnal and annual variation in soil CO_2-efflux can be detected with a limited number of measurement points, but the number of chambers needed to reveal the spatial variation is much higher. The selection of the measurement points should also be unbiased, which requirement is very difficult to reach in practice due to restrictions for chamber installation caused by stones, stems and stumps. The soils in the measured area are glacial tills and the proportion of the stones of the soil volume is often more than 25%.

In the daylight the separation of photosynthesis and respiration from each other can not be done without labelling techniques. Thus the direct respiration measurements are restricted to nighttime only and extrapolation over daytime is needed. This problem can be avoided if the net gas exchange is measured, but to get the amount of soil respiration, a good estimate of the photosynthesis is needed. Based on these restrictions, the estimate of soil efflux can be defined only indicative. The same holds true for shoot respiration and photosynthesis measurements. For the aggregation of the chamber measurements of shoots, models of the amount and vertical distribution of needles and light attenuation are needed in generalizing the results of chamber measurements for values by area (for details, *see* Kolari *et al*. 2009).

The periods of stable atmospheric stratification cause one of the main concerns in the interpretation of the eddy covariance data but the stability-related systematic errors are likely to remain the same from year to year. Due to the stochastic nature of turbulence, half-hourly eddy fluxes suffer from a random error of 10%–20% but over prolonged periods these are practically averaged out. Thus, eddy covariance is in principle able to detect fairly small changes in NEE from year to year although the absolute level might be somewhat biased due to systematic errors in the flux measurement. From April 1998 until June 2000 the eddy covariance measurements were done from a height of 46 m which means that the source area of the fluxes was different from the other measurements which were made at a height of 23 m. The deviation of the carbon accumulation estimates between the EC and the other estimation methods was also highest during these years. The random uncertainty in the annual NEE is generally estimated to be less than 50 g C m^{-2} (Baldocchi 2003). Based on the systematic difference in fluxes observed with two adjacent EC measuring setups, Rannik *et al*. (2006) concluded that the uncertainty in the annual NEE (EC measurements) in SMEAR II station could be as much as 80 g C m^{-2} a^{-1}. The relative error in the annual balances of the flux measurements was estimated to be in the order of 20%–30%.

Comparison of the biomass accumulation and flux measurements

On a general level comparison of the biomass accumulation into trees, the $^{-}$NEE derived from the EC and the chamber derived fluxes of photosynthesis and respiration, gave a similar picture of the carbon balance of the studied ecosystem (Fig. 6), the forest ecosystem studied was a

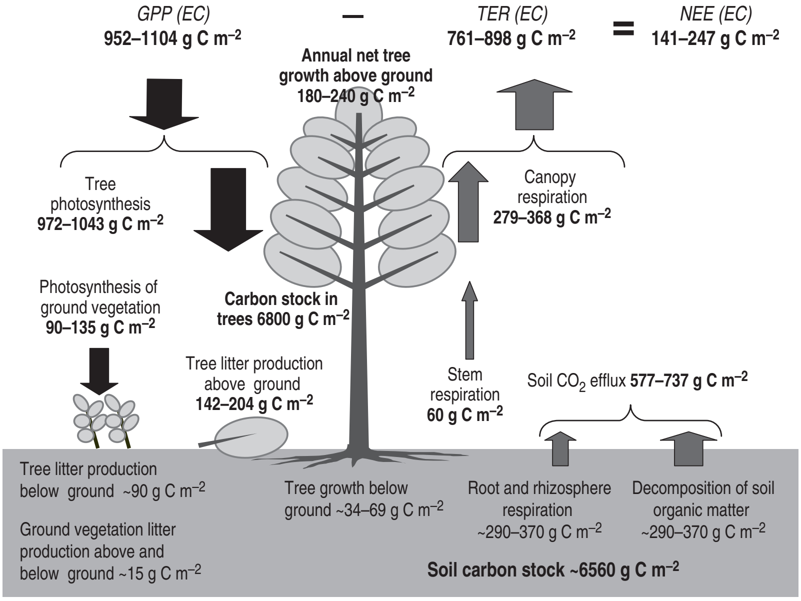

Fig. 6. The carbon balance of the forest in the EC footprint area. GPP, TER and NEE are derived from eddy-covariance measurements, photosynthesis and respiration from the chamber measurements and above ground litter from the litter collector measurements. Annual below ground litter is assumed to equal the amount of needle litter. The annual tree growth is calculated from the measurements of tree dimension and increment cores using biomass functions. Soil CO_2 efflux is based on chamber measurements.

carbon sink throughout the measured period. The annual accumulation of C into tree biomass increased during the measured period and with the distance from the EC mast. The level of $^{-}$NEE based on the EC was lower than the carbon accumulation to the tree biomass in the footprint area with the 200 m radius, but essentially on the same level, when compared with the growth of the trees within a 35-m radius.

The annual average ecosystem GPP derived by EC was 1031 g C m^2. The annual average tree photosynthesis was 982 g C m^2 being slightly lower as the GPP, but when combined with ground vegetation photosynthesis, the combined photosynthesis was 1096 g C m^2 a^{-1} giving somewhat higher values than GPP based on EC. If the annual respiration of soil, shoot and stem was subtracted from the photosynthesis, the estimate of annual accumulation of C was 124 g m^{-2} (Table 6). After 2000, when the measurement height of the EC remained constant, the photosynthesis of the trees showed similar annual trends as the GPP. In this calculation the stand was considered to be a pure Scots pine forest which may introduce a systematic error in the modelled stand photosynthesis.

The annual variation in photosynthetic production of the ground vegetation depends mostly on the photosynthesizing leaf biomass and the available light but also on the temperature and soil moisture (Skre 1975, Skre and Oechel 1981, Williams and Flanagan 1998). According to the biomass estimations the above ground biomass of needles and branches has increased during the measurement period, which may have diminished the proportion of solar radiation that reaches the ground level. In the thinned areas the amount of light reaching the ground vegetation has temporarily increased. The proportion of ground vegetation of the total photosynthesis, which is more than 10%, is so large that it has to be taken into account in the annual carbon balance calculations. The same holds true also for the understorey tree vegetation as the proportion of the total needle and leaf biomass of these plants was high, as compared with their proportion in the total biomass.

When the annual NPP (net primary productivity = net change in biomass + the litterfall above and below ground) is taken from the data of the trees measured close to the EC mast, they gave an estimate of range from 326 to 513 g C m^{-2} a^{-1} which is between 34% and 52% of the estimated range of tree photosynthesis. The NPP/GPP ratio of 0.47 ± 0.04 that Waring *et al*. (1998) proposed as a universal ratio falls well within this range. In the whole measurement area, the accumulation into tree biomass is higher than in the vicinity of the mast, increasing also this ratio if it is assumed that the GPP remains constant. One explanation for the good correlation between $^{-}$NEE (EC) and NPP (biomass) of the closest sample plots is that a large proportion of the EC signal is originating from the near vicinity of the mast. Another explanation could be, as Mäkelä and Valentine (2001) showed, that the ratio between NPP and GPP is likely to vary depending on the age of the trees. The annual accumulation of the tree biomass and the EC measured $^{-}$NEE showed similar annual variation (peaks and depressions) except for the very rainy season in 1998 and the dry summer of 1999. This mismatch can also be related to the change in measurement height in the EC measurements in those years.

The soil respiration was lower than the TER, but if all respiration components are summed together, the combined value is 160 g C m^{-2} higher than the TER. This difference is larger than the annual average difference of 40 g C m^{-2} found in comparison between $^{-}$NEE and biomass accumulation for the 200-m radius footprint area. When the nighttime measurements and a model based on soil temperature were used as the method to produce daily soil respiration, the estimate of the annual soil respiration was in the order of 650 g C m^{-2}. When interpolation between soil efflux measurements and addition of ground vegetation photosynthesis was used in aggregation, the average annual soil respiration was found to be in the range of 700 g C m^{-2}. This is in the high end of the variation for soil efflux derived from the difference method (300–750 g C m^{-2} a^{-1}). Zha *et al.* (2007) concluded that CO_2 efflux from the soil is the dominant component of ecosystem respiration (R_e) in a boreal Scots pine forest. Also in the Scots-pine-dominated ecosystem of this study, soil respiration was the main source of CO_2 efflux.

The possible diurnal variation of R_a due to the diurnal variation in photosynthesis was not taken into account in the temperature model of the soil C-efflux. Bahn *et al.* (2009) showed that in a grassland ecosystem the R_a is higher during daytime. If the phenomenon is similar in woody plants of larger size, the model based on the nighttime temperature and soil CO_2-efflux can give an underestimation of the daytime efflux. When the direct efflux measurements are applied in the integration, the accurate measurements of the ground vegetation photosynthesis is difficult to carry out automatically. In our case, at least during the first years of measurement the rate of photosynthesis of the continuously operating chambers was presumably lower than in the area in general due to the lower amount of vegetation within the chamber. Although the CO_2 efflux rate from cold or frozen soil during the winter is low, the correct estimation of the level of the efflux rate during the period when the automatic chambers are not working properly is important due to the often at least four-month-long period. The different methods used for wintertime CO_2-efflux estimation could give a difference of 100 g C m^{-2} on annual basis. The lowest soil CO_2-efflux values were detected in the driest years, especially in the year 2002.

Soil respiration and litterfall of the current or previous year did not show similar annual fluctuations, which means that the link between litter production and soil respiration is not direct. The annual average above ground litterfall (without thinning effect and branches) was 154 g C m^{-2} which is higher than the average value reported by Ukonmaanaho *et al.* (2008) and Starr *et al.* (2005) for Scots pine stands, but within the range given. If the fine root litter is assumed to be of the same magnitude as the needle litter, the annual fine-root litter would be 92 g C m^{-2}. It is often assumed that the average age of fine roots is one year, but there is also evidence that at least some part of the fine roots may live longer than a year in boreal soils (Withington *et al.* 2006, Tierney and Fahey 2002).

If we assume that in the long run all of the 280 g m^{-2} (variation 225–332) carbon in annual litter is decomposed, this would indicate that the heterotrophic CO_2-efflux corresponds to 45%–72% of the measured soil CO_2-efflux. When calculating the soil efflux of autotrophic respiration as a difference between photosynthesis and other measured components, the range varied between 85 and 412 g C m^{-2} a^{-1}. Högberg *et al.* (2001) showed that large scale girdling decreased the soil respiration by about 50% in the long run, suggesting that the division between the autotrophic and heterotrophic soil CO_2-efflux is 50/50.

The changes in soil-carbon storage could not be measured, and no estimate of carbon accumulation into the soil could be given by soil sampling. However, because in prescribed burning carried out in 1962, a proportion of carbon stored in slash and humus was lost, and because at present a well developed humus layer can be found, it can be assumed that litter accumulation to the site has occurred.

Zha *et al*. (2007) reported four-year results of carbon fluxes in a Sots pine stand of similar age. The respiration of soil and branches was lower than found in our measurements, and although the stem respiration was similar, the chamber measured ecosystem total respiration (731–909 g C m^{-2}) was lower than in this study. Despite the difference in respiration fluxes, the reported GPP (922–1138 g C m^{-2}) and NEP (191–251 g C m^{-2}) were similar to the results found in this study. For a southern boreal treeline aspen forest Griffis *et al*. (2004) presented a carbon accumulation of 300 g C m^{-2}, chamber based respiration in their study was 1315 g C m^{-2} and TER (EC) of 961 g C m^{-2}. In Barford *et al*. 2001, the eight-year annual average $^{-}$NEE was 200 g C m^{-2} and annual average C accumulation to biomass was 160 g C m^{-2}. In their study, the difference between biomass estimate and EC estimate was opposite to our case. Ehman *et al*. 2002 reported 237 and 287 g C m^{-2} NEE for two years with corresponding biomass accumulation of 271 and 377 g C m^{-2}. Urbanski *et al*. 2007 report increasing CO_2 uptake over a 13-year period with the annual variation between 100 and 470 g C m^{-2} with an average annual uptake of 250 g C m^{-2}. The trend shown in their study was similar to the one in our biomass-based carbon sequestration measurements. The NEP in an aspen forest studied by Gough *et al*. (2008) varied between 80 and 198 g C m^{-2}, while the average accumulation into the biomass was 213 g C m^{-2}. In the Finnish national report of greenhouse gases based on national forest inventory, the annual average accumulation of C into tree biomass was ca. 130 g m^{-2} (*see* http://www.stat.fi/tup/khkinv/nir_unfccc_2006.pdf). Although this value is lower than the C accumulation in the forest of this study it fits well with the value observed as it is a national average representing all forest between latitudes 60°N and 70°N.

Conclusions

It is obvious that the measured boreal Scots pine dominated forest ecosystem is at the moment a reasonably large sink of atmospheric carbon. Tree and stand measurements based on diameter at breast height and height were shown to be useful in estimating the amount of biomass and biomass accumulation into trees on a stand level. One of the advantages of this method is that it can be combined with national forest inventories to produce large area estimates. The possibility to analyze the level of uncertainty in the estimate is also valuable.

Both annual measurements of tree dimensions and measurements combined with tree ring measurements gave similar values. However, if the aim is to compare the results of two successive years the estimations based on annual measurements include the risk of getting biased results.

Inaccuracies in the biomass estimations can be caused by the representativity of the biomass equations with regard to the measured stand, concerning especially the assumption of the wood density built into the equations.

The $^{-}$NEE based on EC measurements and tree biomass accumulation gave quite similar results if only the trees in the immediate vicinity of the mast were taken into account, but the biomass accumulation into the trees was higher than the $^{-}$NEE if a larger footprint area was used. In future it might be useful to compare in more detail the biomass accumulation by area and NEE in order to estimate the actual footprint area.

The stable conditions accompanied by low friction velocities lead to an underestimation of the actual NEE. The significance and the role of the advection has not yet been solved.

The proportion of soil respiration is high and thus a correct estimation of this component is essential when the C-balance estimation is based on chamber measured fluxes. Both the spatial and temporal variation of the respiration fluxes can cause large uncertainties in the CO_2 efflux estimate. The aggregation of the result of chamber measurements to estimates by area is in general a challenge.

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Appendix

Heights of the tally trees at the time of the inventory (h) were predicted as a function of the diameter with bark (d) by using height curve of Näslund (1936):

$$h = 1.3 + d^2/(a_{\mathrm{h0}} + a_{\mathrm{h1}}d)^2, \tag{1}$$

where a_{h0} and a_{h1} are fixed parameters.

The linearized height curve was described in the whole data with a mixed model:

$$d_{ki}/(h_{ki} - 1.3) = a_{\mathrm{h0}} + a_{\mathrm{h1}}d_{ki} + v_{\mathrm{h0}k} + v_{\mathrm{h1k}}d_{ki} + e_{\mathrm{h0}ki}, \tag{2}$$

where, d_{ki} is the diameter of tree i on the plot k, h_{ki} is the corresponding tree height, $v_{\mathrm{h0}k}$ is the random constant of plot k, $v_{\mathrm{h1}k}$ the random coefficient of diameter of plot k and $e_{\mathrm{0h}ki}$ the random error of tree i on the plot k. The subscript h indicates the height curve model.

The model for double thickness of bark (b2) was

$$\mathrm{b2}_{ki} = a_{\mathrm{b0}} + a_{\mathrm{b1}}d_{ki} + v_{\mathrm{b0}k} + v_{\mathrm{b1}k}d_{\mathrm{ki}} + e_{\mathrm{b0}ki} \tag{3}$$

where the subscript b indicates the bark model as a function of diameter with bark. The corresponding model as a function of diameter without bark (dw) was

$$\mathrm{b2}_{ki} = a_{\mathrm{bw0}} + a_{\mathrm{bw1}}\mathrm{dw}_{ki} + v_{\mathrm{bw0}k} + v_{\mathrm{bw1}k}\mathrm{dw}_{\mathrm{ki}} + e_{\mathrm{bw0ki}}, \tag{4}$$

where the subscript bw indicates the bark model based on diameter without bark. Other notations in models 3 and 4 are same as in model 2.

The diameters without bark at 1–5(7) years before the inventory were calculated by subtracting the annual diameter growths from the diameter measured in the inventory. The diameter growth without bark was predicted with the model

$$\mathrm{idw}_{ki} = a_{\mathrm{id0t}} + a_{\mathrm{id0}}\,\mathrm{dw}_{ki} + v_{\mathrm{id0}k} + e_{\mathrm{id0}ki}, \tag{5}$$

where the subscript id indicates the diameter increment and a_{id0t} a specific constant for each year. The other notations are same as in the model 2.