

R-06-121

**Modelling carbon and water
flows in terrestrial ecosystems
in the boreal zone – examples
from Oskarshamn**

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December 2006

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Keywords: Mean residence time, Carbon sequestration, Forest ecosystems, Grasslands, Multiple criteria of acceptance.

This report concerns a study which was conducted for SKB. The conclusions and viewpoints presented in the report are those of the authors and do not necessarily coincide with those of the client.

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1 Introduction

Carbon turnover timescales can be used as an approximation of the accumulation of trace elements, such as radionuclides originating from underground, nuclear waste repositories. Thus, depending on carbon and water turnover rates, different ecosystems might be more or less suitable for the location of such repositories. Although both carbon budgets and carbon turnover times have been established for several ecosystems and at several locations, it has been shown that the outcome is highly dependent on climate and the correct estimation of soil respiration; both factors of which are highly site-specific /Medlyn et al. 2005/. It is therefore important to make an analysis of water and carbon budgets and fluxes for each tentative location for a deep repository. By using modelling tools it is possible to incorporate large amounts of empirical data in the estimations of water and carbon turnover. Further more, by conducting a type of sensitivity analysis in the model simulations, an approximation of potential variability in the estimates can be calculated.

The Swedish Nuclear Fuel and Waste Management Co (SKB) are currently investigating two sites (Forsmark and Oskarshamn /SKB 2005ab/) as possible locations for a deep repository of radioactive waste. This study focuses on carbon and water flows in terrestrial ecosystems commonly occurring at both sites. In section three of the report, we present model parameterisations for four hypothetical terrestrial, boreal ecosystems. Carbon turnover in these systems are simulated using a method based on multiple-criteria of acceptance. Secondly, in section four, we apply these parameterisations, with some modifications for site-specific empirical data, on four tentative sites for underground nuclear waste repositories at Oskarshamn. Site-specific data on soil respiration is used as a comparison to simulated values.

Section two and three have, with minor modifications, been published in *Ambio* /Karlberg et al. 2006a/.

2 Model description

The CoupModel is a physically-based, ecosystems modelling package /Jansson and Moon 2001/ that can be used to design a conceptual model for a specific ecosystem /Jansson and Karlberg 2004/. The model describes the interaction between biogeochemical and hydrological processes in a soil-plant-atmosphere system. Fluxes of water, heat, and matter are calculated for a layered soil profile and one or several vegetation layers above with time series of meteorological data as the driving force.

The abiotic part of the model is based on two coupled partial differential equations for the water and heat flows in the soil: the Richard's equation (water) and the Fourier law of diffusion (heat), respectively /Jansson and Halldin 1979/. Surface boundary conditions, such as evapotranspiration, soil surface temperature, and snow melt are estimated from energy balance calculations where net radiation is balanced by turbulent fluxes of sensible and latent heat, and surface heat flow /Alvenäs and Jansson 1997, Gustafsson et al. 2004/. Water uptake from the soil is based on a soil-plant-atmosphere-continuum approach, considering the flux of water from the soil through the plant as a response to the demand of water from the atmosphere, i.e Penman-Monteith equation /Penman 1953, Monteith 1965, Lindroth 1985/. Snow accumulation and melt are described, as well as the partitioning between infiltration to the soil or surface runoff at the uppermost soil boundary.

The biotic part of the model simulates plant growth, as well as carbon and nitrogen turnover in the soil /Johnsson et al. 1987, Eckersten et al. 1998/. Biomass is partitioned into several aboveground and belowground pools of carbon and nitrogen. Gross production of carbon (GPP), driven by solar radiation /Monteith 1977/ and regulated by leaf nitrogen content, water uptake, and air temperature, is allocated to different compartments of the plant; leaves, stem, coarse roots, and fine roots, according to pre-specified patterns. Each compartment is assumed to have a potential carbon to nitrogen ratio, which subsequently gives rise to a nitrogen demand. Plant respiration is partitioned on growth and maintenance respiration from all plant compartments /Karlberg et al. 2006b/. Daily litterfall is calculated as fractions of above-ground and below-ground parts of the plant entering the soil organic pools. Two pools of different turnover rate were used to represent the soil organic material, called litter and humus. The most important inputs to the biotic part are thus characteristics governing the plant life-cycle such as allocation patterns, plant assimilation and respiration, nutrient uptake by plants, external nitrogen inputs to the soil, and finally decomposition and redistribution of different decomposition products in the soil profile.

The most central component for interaction between the biotic and the abiotic parts of the CoupModel is the leaf area index (LAI), which governs both interception of radiation and of precipitation. Both the losses of water and carbon from the soil by either transpiration or respiration, are strongly related to temperature and moisture of the soil.

3 Carbon turnover in four hypothetical terrestrial ecosystems

3.1 Ecosystem description

Four terrestrial ecosystems were selected to represent the hypothetical systems included in the study (Table 3-1). These systems were selected both because they are likely to differ in terms of carbon turnover times, and also because together they are commonly occurring in southern and central Sweden. The first ecosystem, a semi-natural grassland, is characterised by the lack of a tree layer, and a field layer consisting of a mixture of grasses and herbs growing on clay. A forest dominated by alder (*Alnus glutinosa*) with a high groundwater table was chosen to represent the second ecosystem. This deciduous tree has symbiotic nitrogen-fixating bacteria in its root nodules. Due to the ample supply of nitrogen, it only retains a small fraction of its nutrients before shedding its leaves in the autumn. The field layer was characterised by nitrophilic, lush grasses and herbs growing on a wet organogenic soil type. A pine forest (*Pinus sylvestris*), growing on a thin layer of till with a field layer dominated by cowberry, was chosen as the third ecosystem in the study. Another coniferous forest on till was selected to represent the fourth ecosystem; in this case Norway spruce (*Picea abies*). In this forest, the field layer consisted mainly of blueberry and some broad-leaved grasses. Lastly, a managed forest similar to the Norway spruce ecosystem in composition was also included in the study as a comparison to the natural ecosystem. Management was assumed to follow the general practice for southern Sweden as recommended by the Swedish Forest Agency /Swedish Forest Agency 2005/. Thus, the managed spruce forest was cleared after 15 years, resulting in a removal of 60% of the tree biomass, which was left in the forest as litter. In addition, the forest was thinned after 40 and after 80 years, affecting 25% of the tree biomass. Whereas leaves, coarse roots and fine roots remain at the site to form litter, 80% of the stem biomass (of the trees affected by thinning) is removed. The field layer was assumed to be unaffected by these operations.

3.2 Parameterisation and model application

A number of parameter values characterising the ecosystems were derived from the literature; either values from field measurements or from modelling studies (Table A1). These parameters described, for example, carbon allocation in the plant, maintenance and growth respiration, nitrogen demand and plant litterfall, and were called primary parameters. Some of those were plant or soil specific, whereas the rest were of a more general nature and were therefore assumed to be the same for all systems. The parameterisation of the field layer in the alder forest was used to represent the grassland vegetation. For each ecosystem there were also a number of parameters that could not easily be determined from the literature, so called secondary

Table 3-1. Description of the main characteristics of the ecosystems included in the study.

Name	Tree layer	Field layer	Soil type	Management
Grassland	none	Grass and herbs	Clay	None
Alder	Alder (<i>Alnus glutinosa</i>)	Grass and herbs	Peat	None
Pine	Scots pine (<i>Pinus sylvestris</i>)	Cowberry (<i>Vaccinium vitis-idea</i>)	Till (thin)/ bedrock	None
Spruce	Norway spruce (<i>Picea abies</i>)	Blueberry (<i>Vaccinium myrtillus</i>)	Till	None
Spruce, managed	Norway spruce (<i>Picea abies</i>)	Blueberry (<i>Vaccinium myrtillus</i>)	Till	Clearing, thinning and harvest

parameters (Table A2). Instead, a range of values was specified for each of them, assuming that the “true” value would lie somewhere within that range. Random numbers were generated for each secondary parameter within the respective range of values.

One hundred simulations were run for each ecosystem with the primary parameters and using the pre-generated random numbers as secondary parameters. Simulations were based on a one-year data-set containing hourly climatic data from a meteorological station at the northern part of the Öland island (57°N'22''1.3, 17°E'5''43.4) 1981 /Larsson-McCann et al. 2002/, scaled to be representative for the SKB study area in Äspö, Oskarhamn. This data was recycled and used as driving data for 100-year simulations. The reason for choosing such a long simulation period was to insure that soil and plant carbon remained stable in the natural ecosystems. Another reason was that 100 years is the approximate rotation period for a spruce production forest in southern Sweden. Consequently, the initial carbon contents in the plant and soil was parameterised according to average carbon plant and soil levels in natural ecosystems, except for in the managed forest ecosystem, where the initial plant carbon content was chosen to represent a newly planted tree. Simulations were compared to pre-specified criteria of acceptance including both site specific and generic data (Table A3–A5). An error function adopted from Barrett /Barrett 2002/ was used to find the best parameters sets with respect to all criteria of acceptance:

$$E = \sum_{i=1}^M w_i \left(\sqrt{(s_i - o_i)^2} / (o_{\max} - o_{\min}) + p_i \right)$$

where s_i is a simulated value, o_i , o_{\max} , and o_{\min} , are the pre-specified optimum, maximum, and minimum values allowed for a specific criteria, respectively, p_i is a penalty factor that is 1 if s_i is outside the maximum and minimum range (otherwise 0), and w_i is a weighting factor taking values between 0 and 1, which was used to weight the importance of different criteria. The ten simulations with the lowest error function were used in the analysis to calculate average and standard deviation of the secondary parameters, and of the simulated carbon budgets (Table A2).

3.3 Results

Carbon storage varied by a factor two between ecosystems (Figure 3-1). The alder ecosystem had the highest total carbon content (25,000 gC m⁻²) of all systems, closely followed by the natural spruce forest (18,000 gC m⁻²). Grassland, pine and managed spruce all had about the same total carbon storage (around 13,000 gC m⁻²). Looking instead at the distribution of carbon within the systems, similarities exist between the grassland and the alder systems, where the majority of the carbon in the system was located in the soil biomass (97% and 73% respectively). On the contrary, in the ecosystems dominated by coniferous trees, the plant biomass consisted of about half of the total carbon storage. A comparison between the natural and the managed spruce ecosystems shows that the soil was rather similar in the two systems, whereas the plant biomass was lower in the production system. The variability in the estimations of carbon storage can be assessed by studying the ratio between the standard deviation and the mean, for different parts of the systems. For the soil in all systems this figure was rather low (7–8%), while the tree biomass estimations had a larger variability (12–26% for all systems) (Figure 3-1). The largest variability was found in the estimates of the field layer biomass (24–75% for all systems).

Total fluxes of carbon in and out of the ecosystems also varied by a factor two between ecosystems (Figure 3-1). The alder and the natural spruce forest had the highest carbon fluxes (around 1,600 gC m⁻² yr⁻¹), followed by pine (1,000 gC m⁻² yr⁻¹) and lastly the grassland (600 gC m⁻² yr⁻¹). Since the production system is not in steady-state, the influx of carbon exceeded the efflux by about 100 gC m⁻² yr⁻¹. The uncertainties in the estimations of the fluxes were generally greater compared with the storages, but showed a similar pattern. Thus, the ratio

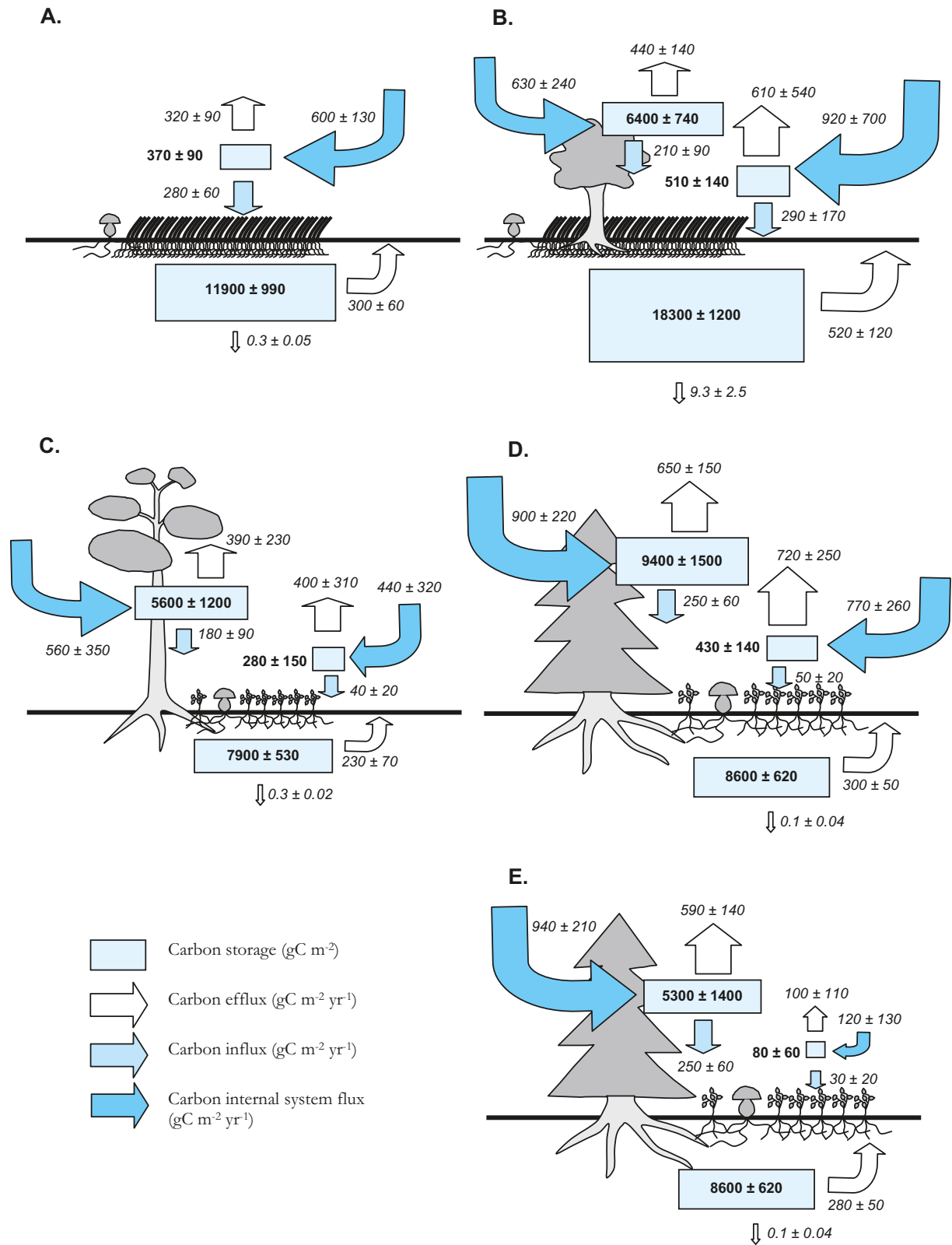


Figure 3-1. Carbon budgets for the hypothetical ecosystems. a) grassland b) alder c) pine d) spruce and e) spruce managed forest. Carbon storages (gC m⁻²) in bold and carbon fluxes (gC m⁻² yr⁻¹) in italics, including standard deviations.

between the standard deviation and the mean for soil heterotrophic respiration varied between 17–30%, while the corresponding figures were 22–59% and 22–110% for the tree and the field layer (excluding grassland) respectively (Figure 3-1). The grassland and the natural spruce forest generally had lower variability in the estimation of fluxes compared to the rest.

Mean residence time (MRT), that is the average time an assimilated carbon molecule stays in a certain part of system before being discharged or respired, was calculated for the above and below ground parts of the trees and the field layers, as well as for the litter and humus fractions of the soil (Figure 3-2). The lowest MRT was found to be in the field layer (approximately one year). In comparison, trees had an MRT of ten years, which thus is significantly higher. However, if the turnover time in trees is calculated for above and below ground parts separately, the picture is altered (Figure 3-2). Above ground MRT for trees was 25 years on average, while the corresponding figure for the below ground tree components was less than two years. There was also a large difference between the MRT for litter and humus (Figure 3-2). While the former had an MRT of less than two years, the MRT in humus was found to be approximately 150 years. On average, total MRT for the entire ecosystem was around 15 years.

Variability in the estimations of MRT was greatest for the field layer, in particular in the pine, alder and production ecosystems, while it was lowest for the soil components. Despite this variation in the MRT estimations, some differences between the ecosystems could be identified (Figure 3-2). For instance, the MRT of the below ground tree biomass was more than two times higher in the coniferous ecosystems (1.7 years) compared to the alder (0.7 years). Furthermore, the MRT of the field layer vegetation was about 2.5 times higher for the managed spruce forest compared to the natural spruce ecosystem, both above ground and below ground. MRT of the field layer vegetation also differed between the natural pine and spruce ecosystems, where the former had both higher mean values and standard variations. Finally, MRT for the humus pools varied between 135 years for the natural spruce forest to 165 years for the alder forest, whereas the MRT for the litter pool varied very little between the ecosystems (ranging from 1.8 years to 2.3 years).

To assess the uncertainties in the simulated carbon budgets and differences between the ecosystems, it is important to recognise the number and types of criteria met. When aggregated into groups, the percentage of criteria fulfilled in the final simulations showed a similar pattern within the ecosystem, with two exceptions: alder and grassland (Table 3-2). The alder system had a lower number of fulfilled criteria, especially with regards to the tree layer and litterfall.

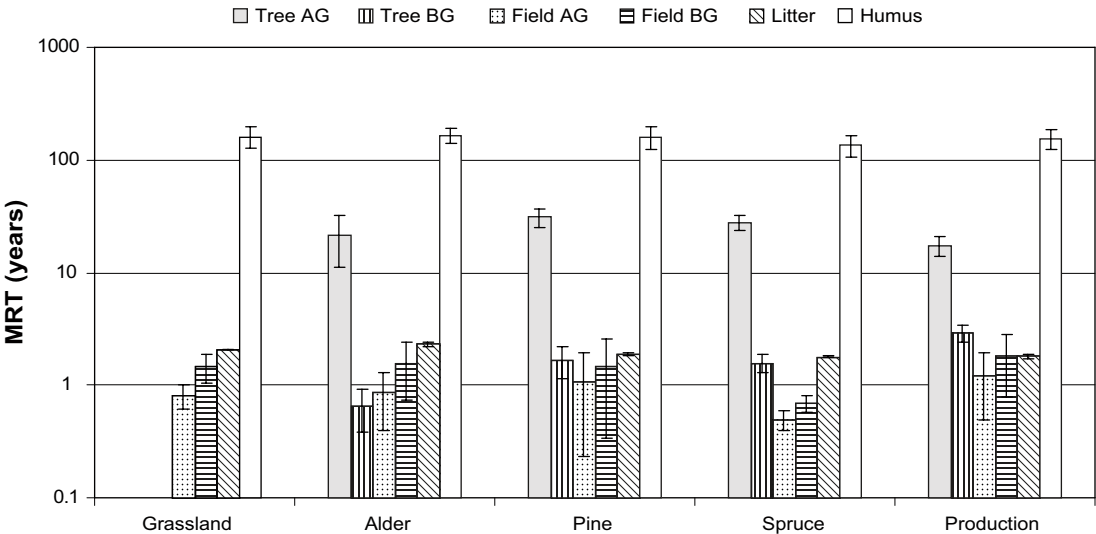


Figure 3-2. Mean residence time of carbon in different parts of the ecosystems; tree layer and field layer are separated on above ground and below ground components, and the soil organic carbon is separated on the fast “litter” pool and the slow “humus” pool according to the simulations. AG = above ground, BG = below ground.

Table 3-2. Average percentage of fulfilled criteria in the best simulations selected through the multiple criteria parameterisation method. The 30–45 criteria for model acceptance have been aggregated into groups of similar nature.

	Carbon storages			Carbon flows			Miscellaneous		
	Soil	Tree	Field	NPP ²	Respiration	Litterfall	LAI ³	N processes	Water flows
Grassland	95	n.a.	78	75	100	20	50	100	n.a.
Alder	100	67	46	43	55	8	70	66	n.a.
Pine	100	93	66	48	40	40	50	54	n.a.
Spruce	100	90	74	47	50	28	45	96	n.a.
Spruce m¹	100	80	66	50	25	42	60	81	58
Mean	99	83	66	53	54	28	55	79	58

¹Managed forest. ²Net primary production. ³Leaf area index.

In contrast, the grassland simulations performed better over all than the average. Generally, criteria related to carbon storages in the tree layer and in the soil, as well as nitrogen processes, were fulfilled to a higher extent compared to criteria related to respiration, litterfall, and leaf area index, which had a poorer over-all result in all ecosystems.

3.4 Discussion

Due to the wet conditions in the alder ecosystem, decomposition of carbon is slow, resulting in large carbon storage in the soil. The high total carbon content in the natural spruce ecosystem could instead be attributed to the high carbon content in trees. Fluxes of carbon to and from the ecosystems were also greatest for the spruce and alder ecosystems. In the alder ecosystem, the high productivity is due to the ability of the tree to fixate nitrogen. Because of nitrogen-rich litterfall from the tree, nitrogen levels in the soil are high, which is reflected in low C/N ratios. The field layer benefits from these high nitrogen levels, causing a high productivity in the field layer as well. On the contrary, the trees and the field layer compete strongly for nitrogen in the coniferous ecosystems. Therefore, in the spruce ecosystem it is instead high leaf area indices that generate a high productivity. Mean carbon content in the tree over its one hundred year lifespan in the managed forest is low compared with trees in the natural spruce forest. This is due to the fact that the mean value for the managed forest also includes period from when the tree was planted until it reached maturity. Furthermore, the field layer in the production forest is lower compared with the natural forest. Most likely, this is an effect of a high tree leaf area index in the production system, resulting in light stress for the field layer.

Because the size of the storage pools in relation to the fluxes were of the same order of magnitude in all systems, the MRTs consequently turned out to be very similar. Although the MRT for the whole ecosystem was around 15 years, MRT varied drastically depending on the route of carbon through the ecosystem. Not surprisingly, the highest turnover rates were found in the field layer. The field layer turnover rates were slightly higher in the natural spruce forest compared to the managed spruce and the natural pine, mainly as a result of the relatively low field layer production in these latter ecosystems. Generally, above ground MRT was higher than below ground MRT for trees in all ecosystems, due to a slow turnover of carbon in the stems. Another interesting aspect on turnover in the different trees was the lower MRT of the below ground biomass in alder, which probably was a reflection of the higher root activity in the nitrogen fixating system. Carbon that does not leave the plants through respiration continues through the system to the soil where it forms litter. Litter is quickly decomposed resulting in another respiratory loss of carbon from the system. The remaining material forms humus, which has an estimated turnover time of more than one hundred years. The variation of simulated MRT between ecosystems for the humus pools can be explained by different soil temperature and soil moisture regimes (not shown) in combination with the parameter values for humus

decomposition (Table A2). In conclusion, the turnover time for an atom of carbon and associated trace elements such as radionuclides entering the ecosystem can vary between one to more than one hundred years. If the fate of radionuclides is of interest, it is thus of importance to know not only how much is assimilated into the biomass, but also how the trace elements are allocated to different parts of the system in order to predict the turnover time of the trace elements. To make it even more complex, the allocation and decomposition patterns may differ between trace elements and carbon. However, the present simulation of the carbon turnover patterns in the five selected ecosystems may be a starting point for a more elaborate analysis of trace element turnover.

The major uncertainties in simulated carbon budgets as well as in the model parameterisations, were related to carbon fluxes, i.e. photosynthesis, respiration and litterfall. This was evident from the large standard deviation in the simulated fluxes, and in the relatively low number of criteria met for respiration and net primary production compared to the other groups of criteria. Nonetheless, we believe that an acceptable level of fulfilled criteria was achieved for all ecosystems in order to draw conclusions on the variation of behaviour within and between these systems. Carbon budgets for boreal ecosystems are characterized by a small net exchange as a result of large inflows and outflows. For such ecosystems, it is of high importance to have well-defined criteria, not only with regards to the relationship between the inflows and outflows of carbon, but also on the absolute levels, to avoid over-parameterisations. The estimated turnover times for the woody part of the trees (approximately 20–30 years), may be too high compared to other studies /e.g. Barrett 2002/, which indicates that respiration as well as assimilation of carbon may have been overestimated. On the other hand, the turnover time of about 150 years in the slowly decomposing soil organic matter (humus) is well within the range of reported values /e.g. Schulze et al. 2005/. Net ecosystem carbon flux data were missing in this study, which could have improved the parameterisation of the plant and soil respiration. On the other hand, the resulting carbon budgets for the spruce ecosystem were similar to those presented by for instance Medlyn and co-workers /Medlyn et al. 2005/, who reported a total system respiration of about 900–1,600 gC m⁻² yr⁻¹ comparing spruce and pine forests in Sweden, UK, and France. Similarly, the total system respiration from an alder forest in Germany was estimated to be about 1,800 gC m⁻² yr⁻¹, which is just slightly higher than those reported in this study /Kutch et al. 2001b/.

This study demonstrated a method for how to identify crucial ecosystems behaviour using a detailed process oriented model. The model was successfully combined with climatic data from one site and a number of different data sources to provide consistent descriptions of carbon fluxes for different terrestrial ecosystems. Obviously, the criteria for model acceptance could be designed in many ways and the basic functional differences between the assumed parameter settings could be discussed. The criteria were to some extent subjectively chosen and could not easily be fulfilled by comparison with independent data. However, the approach was operational and transparent when synthesizing knowledge from many different sources and investigations. Obvious problems are that the period of simulation is very long and that the ecosystems are to a large extent only simplified representations of possible real ecosystems. This means that a conventional validation and calibration of model parameters is not a realistic alternative. The description of carbon turnover in the different ecosystems provided a frame for a dual understanding of the model design: first of the consequences of the interaction between processes described in the model, and secondly of the ability of the model to estimate important characteristics such as turnover time in different components of the ecosystems. Furthermore, the parameterisation derived from this study could directly be used for different types of simulation experiments, such as the impact of different land use practices on the transport and retention of different radionuclides. In order to understand trace element turnover in terrestrial ecosystems it is important to recognise not only the dilution and allocation in the biomass following carbon assimilation by the plant and turnover in the soil, but also plant water uptake from the soil with its associated trace element uptake. Investigations were the link between trace element turnover and fluxes of both water and biomass in the soil-plant system is crucial could benefit from the type of model descriptions presented in this study.

4 Carbon and water budgets at four sites located within the Oskarshamn study-area

4.1 Ecosystem description

Four sites located within the Oskarshamn study-area were included in this part of the study: a semi-natural grassland on a fine sand with a high soil organic matter content, an alder forest on peat, a managed spruce forest on peat and finally a pine forest on till (Table 4-1). All ecosystems are similar to the corresponding hypothetical systems described in the previous section in terms of the vegetation cover, but differs in soil nitrogen and carbon composition.

4.2 Parameterisation

Measured data on soil carbon and nitrogen content at each site was used to parameterise the initial conditions of the litter and humus pools in the site-specific simulations. Total soil respiration (autotrophic and heterotrophic) at the grassland, spruce and pine forest sites was measured monthly from March 2004 to March 2005 (Tagesson unpublished data). These measurements were used to calibrate the simulations by adjusting the groundwater level, since this variable was unknown. Due to different exposure to oxygen, a change in groundwater level predominantly affects heterotrophic respiration and has a large impact on soils rich in organic matter such as those at the study-site.

To create reasonable initial conditions at the beginning of the soil respiration measurement period in 2004, simulations were started from 1993 and ended in July 2005. Climatic variables were measured at Äspö meteorological station, about 30 km from the study area /SKB 2005c/. Hourly data on precipitation, air temperature, global radiation, wind speed and relative humidity was available from 2003-09-09 to 2005-07-07. From this data-set the variables from 2004 were replicated several times to create a longer time-series ranging from 1993-01-01 to 2003-09-09. These two data-set were then combined to form a continuous series from 1993-01-01 to 2005-07-07.

In order to get an estimate of the variance in the different parts of the carbon budgets, the relative variance (i.e. the standard deviation divided by the mean) estimated for the hypothetical systems was multiplied with the mean values from the site-specific simulations. Carbon turnover was not calculated for the site-specific ecosystems since none of them were found to be in steady-state. Since the depth of the organic layer was not known, only the organic content in the uppermost meter of the soil is shown in the results.

Table 4-1. Description of the main characteristics of the ecosystems included in the study.

Name	Tree layer	Field layer	Soil type
Grassland	none	Grass and herbs	Clay
Alder	Alder (<i>Alnus glutinosa</i>)	Grass and herbs	Peat
Pine	Scots pine (<i>Pinus sylvestris</i>)	Cowberry (<i>Vaccinium vitis-idea</i>)	Till (thin)/bedrock
Spruce, managed	Norway spruce (<i>Picea abies</i>)	Blueberry (<i>Vaccinium myrtillus</i>)	Peat

4.3 Results

Soil respiration was generally well described in the model simulations (Figure 4-1). For the grassland, the main deviation between simulated and measured values occurs in August and September (Figure 4-1a). During these months simulated values far exceed measurements, causing the annual simulated mean to be higher than the measured (3.45 and 2.89 $\text{gC m}^{-2} \text{day}^{-1}$ respectively). Nonetheless, the agreement between simulated and measured values was still quite high ($r^2 = 0.72$). Simulated soil respiration in the pine forest was overestimated during the winter months whereas during summer, it was sometimes underestimated (Figure 4-1b). This caused the simulated annual mean soil respiration to be somewhat large (3.87 $\text{gC m}^{-2} \text{day}^{-1}$, compared with the measured 3.17 $\text{gC m}^{-2} \text{day}^{-1}$), and the overall agreement between simulations and measurements was lower than for the grassland ($r^2 = 0.60$). The best correlation was found for the spruce forest, in which simulated soil respiration agreed well with measurements throughout the entire year ($r^2 = 0.85$) (Figure 4-1c). Mean annual soil respiration in the simulation was 2.72 $\text{gC m}^{-2} \text{day}^{-1}$ compared with 2.55 $\text{gC m}^{-2} \text{day}^{-1}$ measured in the forest.

Carbon budgets were estimated for each ecosystem based on the results from the simulations (Figure 4-2). Compared with the hypothetical ecosystems, the site-specific systems had larger fluxes of carbon to and from the system. Due to the high organic content in the soils, the vast majority of carbon is located below ground in all ecosystems. None of the ecosystems are in steady-state in terms of carbon storage (Figure 4-2). For the grassland, the annual average net ecosystem exchange¹ is about -600 gC yr^{-1} , while it is close to zero in the spruce forest (-80 gC yr^{-1}) and is positive in the alder and pine forests (230 gC yr^{-1} and 200 gC yr^{-1} respectively). Soil organic content decreases annually in the grassland and the spruce forest, while it increases in the alder forest and remains stable in the pine forest. In all ecosystems, the carbon content in the vegetation layer either increases or remains rather stable.

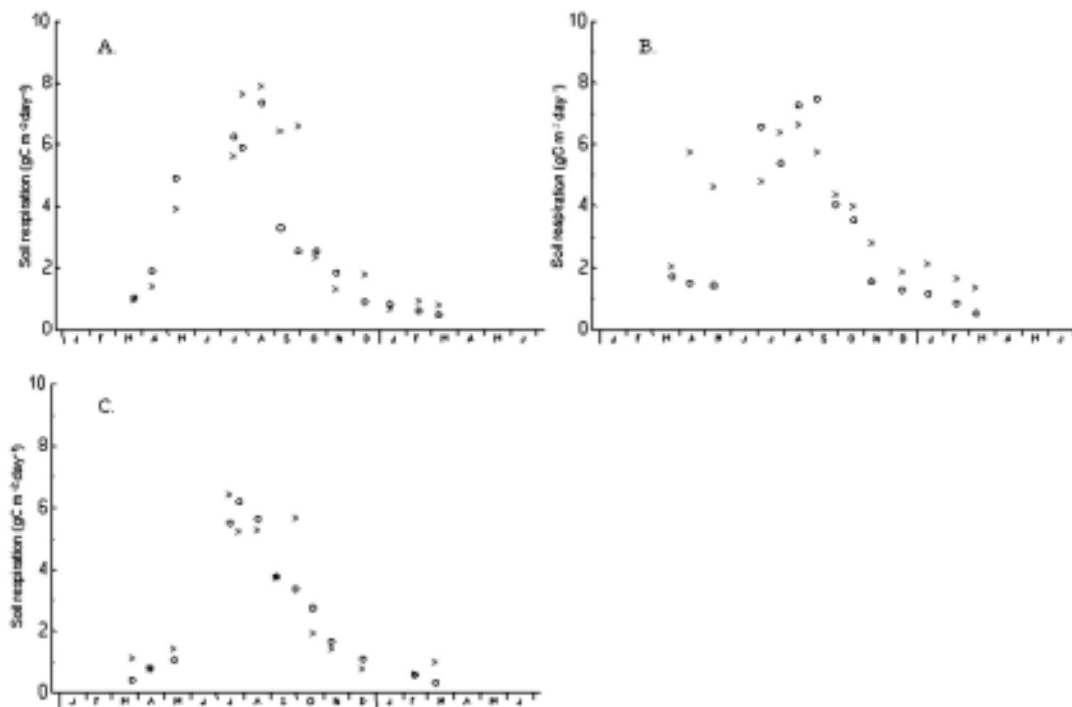


Figure 4-1. Simulated (crosses) and measured (open circles) soil respiration from March 2004 to March 2005. Hourly mean values measured during daytime.

¹ A negative sign indicates a loss of carbon from the system.

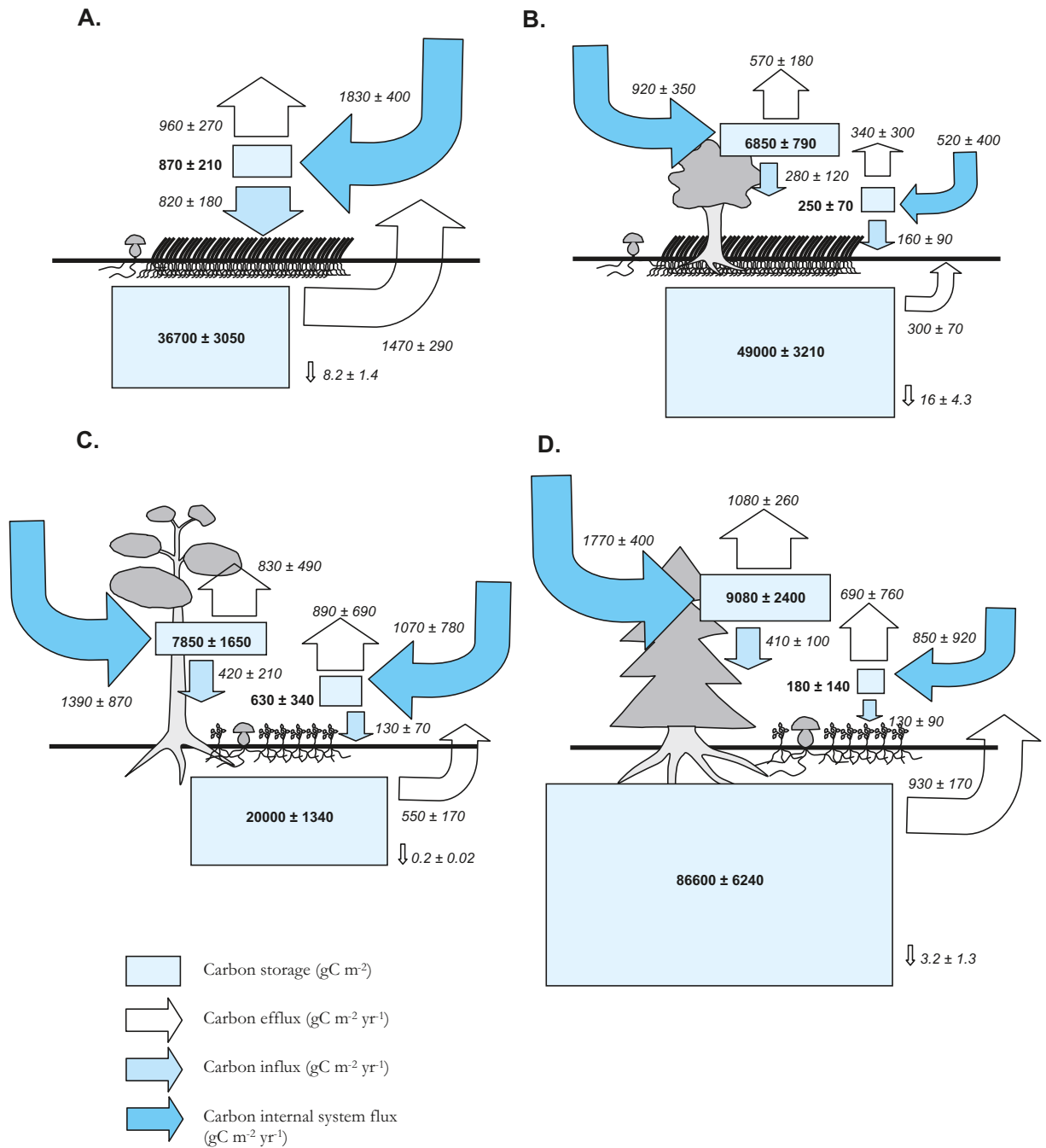


Figure 4-2. Carbon budgets for the site-specific ecosystems located within the Oskarshamn study area. a) grassland b) alder c) pine and d) spruce managed forest. Carbon storages (gC m⁻²) in bold and carbon fluxes (gC m⁻² yr⁻²) in italics, including standard deviations estimated from Figure 3-1.

Annual water flows were estimated in the simulations (Figure 4-3). These estimates show that most of the water entering the ecosystems as precipitation leaves as subsurface drainage or surface runoff, except in the alder forest. This is particularly true for the grassland and the pine forest, in which evapotranspiration is about 30% of incoming precipitation. The corresponding figure is around 45% for the spruce forest. In the coniferous forests surface runoff exceeds drainage, while the opposite holds true for the grassland and alder forest. Despite a very low interception evaporation, total evapotranspiration in the alder forest is about 50%. A very high soil evaporation constitutes the majority of that figure.

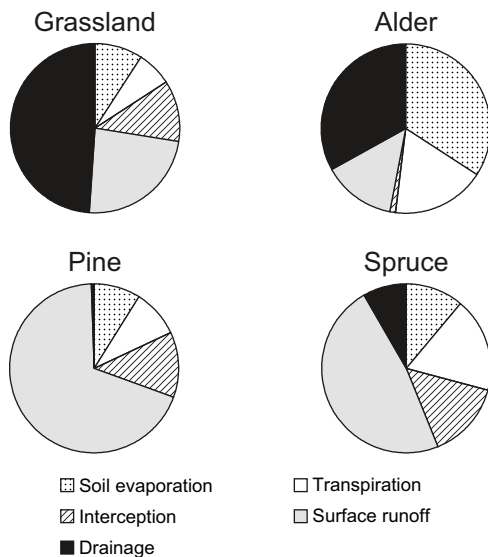


Figure 4-3. Participation of incoming precipitation for the site-specific ecosystems located within the Oskarshamn study area.

4.4 Discussion

Simulated soil respiration was fitted to measurements by adjusting the groundwater level, which predominantly affected heterotrophic respiration. By doing so, it was possible to affect the annual mean rate of soil respiration, but not the dynamic behaviour of simulated soil respiration over the whole year. Despite this, the simulated development of soil respiration over the year showed a high correlation with measurements, as indicated by the high r^2 -values. Hence, the model seems capable of accurately describing soil respiration processes within the year. The lowest correlation was found in the pine forest, which is probably due to difficulties related to estimating soil water fluctuations and surface runoff in a patchy terrain.

Compared with the hypothetical ecosystems, the site-specific systems differed predominantly in soil composition. All soils from the Oskarshamn study-area were very rich in organic matter, and soil respiration was high at all measured sites. The estimates from the simulation indicates that as much as 80% of total soil respiration is heterotrophic respiration in the grassland. For the spruce and pine forests the corresponding figures were 45% and 35% respectively. A rapidly decreasing carbon content in the soil at the grassland site, indicates that the area recently has been drained, thereby exposing non-decomposed carbon to aerobic conditions leading to high rates of heterotrophic respiration. A similar situation seems to prevail at the spruce forest site, although at a much lower rate. This site is still rather wet, resulting in a much lower decrease in soil carbon content compared to the grassland. At both sites, the soils will continue to loose carbon until most carbon above the groundwater level has been decomposed. If further drainage is imposed, more non-decomposed carbon will be exposed depending on the depth of the peat layer of the soil. Another effect of this process is a natural fertilisation of the soil. As carbon dioxide is transferred to the atmosphere, nitrogen is left behind in the soil. This was seen in the simulations both at the grassland and the spruce forest sites as a high rate of photosynthesis. The soil at the pine forest site seems stable in terms of carbon content. Compared with the hypothetical forest, this soil is richer in nitrogen content, which causes plant growth to be significantly higher. The high growth rate also contributes to high soil respiration rates. Due to very wet soil conditions, the soil in the alder ecosystem is the only soil that increases in carbon content over time; however, since neither soil respiration nor groundwater level were measured at this site, this should only be considered as a rough estimate.

The simulated carbon budgets can also be compared to descriptive models on carbon from three of the different ecosystems in Oskarshamn, but with slightly different soil conditions /Löfgren et al. 2006/. Due to the rapid combustion of soil carbon in the grassland simulations and the concurrent fertilisation of the soil, NPP, biomass carbon content and consequently also litterfall becomes very large, compared with the descriptive model. It is possible that the current model design and parameterisation tends to cause an exaggerated impact of soil nitrogen on plant growth. Heterotrophic soil respiration was also larger in the simulations compared with the descriptive model, which may partly be explained by a slight overestimation of total soil respiration in the simulations. Despite this, simulated heterotrophic respiration is still larger than in the descriptive model. However, if heterotrophic respiration was to be lowered in the simulations, root respiration had to be increased substantially in order to correlate total soil respiration with measurements. Thus, it is possible that soil heterotrophic respiration is slightly underestimated in the descriptive model. In the pine forest ecosystem simulation, the relatively low nitrogen stress causes biomass, NPP and litterfall to be high compared with the descriptive model by Löfgren and co-workers /Löfgren et al. 2006/. Similar to the grassland, soil heterotrophic respiration is high in relation to the values given in the descriptive model. Finally, the simulated spruce ecosystem was compared to a corresponding system described by Löfgren and co-workers /Löfgren et al. 2006/. While both NPP and litterfall were similar in the simulations and the descriptive model, soil heterotrophic respiration was again higher in the simulations. Dissolved organic carbon was of the same order of magnitude in all ecosystems in both the simulations and the descriptive models. To conclude, the biomass carbon content and the associated variables NPP and litterfall, are dependent on the nutrient status of the soil, which seemed to differ between the simulations and the descriptive models. Heterotrophic respiration is high in the simulations compared with the descriptive models, which might be a reflection of the difficulty in separating heterotrophic respiration from total soil respiration. Hence, it seems that both models describe the carbon budgets of the ecosystems in a similar way.

In the grassland ecosystem, low evapotranspiration is caused by low transpiration since there is only one transpiring vegetation layer. A lot of water infiltrates in the soil and leaves the system as subsurface drainage. The alder forest is instead characterised by very wet conditions in low-land terrain. This causes a high soil evaporation and a rather low surface runoff. Interception evaporation was probably underestimated in the model simulations, but on the other hand, transpiration might have been exaggerated since it was not affected by the negative impacts from prolonged water logging. Surface water conditions were difficult to portray in the pine forest simulations, since the terrain is heterogeneous, consisting of a thin soil cover interspaced with bare rock. These conditions cause a large surface runoff of water while drainage is close to zero due to nearly impermeable bedrock. Both trees and field layer regularly face water stress conditions, leading to relatively low transpiration levels. In the spruce forest, wet soil moisture conditions were rather favourable for transpiration, thus giving rise to fairly high transpiration rates. The high groundwater table also caused high rates of surface runoff while drainage remained relatively low.

5 Conclusion

Carbon budgets and mean residence times were estimated in four hypothetical ecosystems. The greatest uncertainties in the estimations lie in the calculation of fluxes to and from the field layer. A parameterisation method based on multiple criteria, synthesising a wide range of empirical knowledge on ecosystem behaviour, proved to be useful both in the estimation of unknown parameters, to demonstrate model sensitivity, and to identify processes where our current knowledge is limited. The parameterisations derived from the study of the hypothetical systems were used to estimate site-specific carbon and water budgets for four ecosystems located within the Oskarshamn study-area. Measured soil respiration was used to calibrate the simulations. An analysis of the simulated carbon fluxes indicated that two of the ecosystems, namely the grassland and the spruce forest, were net sources of carbon dioxide, while the alder and the pine forest were net sinks of CO₂. In the former case, this was interpreted as a result of recent drainage of the organogenic soils and the concurrent increase in decomposition. The results from the study conformed rather well with results from a previous study on carbon budgets from the Oskarshamn study area.

Acknowledgement

A number of persons have contributed to this report. Magnus Svensson, KTH, has been helpful with providing useful literature references, and has shared his knowledge in ecosystems modelling of boreal forests. Annika Nordin, Tryggve Persson, Bengt Olsson and Tom Ericsson, SLU and Umeå Plant Science Centre, kindly provided data for the parameterisation of the ecosystems. Anders Löfgren, Tobias Lindborg and Ulrik Kautsky, SKB, have also been helpful with providing site-specific data from Oskarshamn for the simulations. Anders Lindroth and Torbern Tagesson, Lund University, shared their soil respiration measurements for the second part of the study. Finally, Clare Bradshaw, Stockholm University, commented on parts of a previous version of the manuscript. SKB provided the funding for this study.

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Table A1. Differences between plant types, primary parameters.

Property	Spruce	Pine	Alder	Blueberry	Cowberry	Grass/herb	Unit	Ref.
Photosynthesis and resp.								
Radiation use efficiency ¹	8	8	8	8	8	8	gDwMJ ⁻¹	/Charles-Edwards et al. 1986/
Optimum temp. interval	10–25	15–30	15–25	10–20	10–20	10–20	°C	/Hoffmann 1995, Strand et al. 2002, Larcher 2003, Peng and Dang 2003/
Min/max temp	–4/40	–5/40	–2/40	–2/40	–2/40	–2/40	°C	/Hoffmann 1995, Larcher 2003, Peng and Dang 2003/
Optimum C/N ratio, leaf	24	24	11	24	24	11	–	/Wikström and Ericsson 1995/
Threshold C/N ratio, leaf	77	77	77	cal.	cal.	cal.	–	/Field and Mooney 1986, Wikström and Ericsson 1995/
Growth resp. ²	0.21	0.21	0.21	0.21	0.21	0.21	gC gC ⁻¹	/Chung and Barnes 1977, Linder and Troeng 1981, Penning de Vries and van Laar 1982/
Maint. resp. stem ³	0.00015	0.00015	cal.	cal.	cal.	cal.	day ⁻¹	/Kinerson et al. 1977, Linder and Troeng 1981, Bossel 1996/
Maint. resp. fine roots	0.006	0.006	cal.	cal.	cal.	cal.	day ⁻¹	/Linder and Troeng 1981, Bossel 1996/
Allocation								
Root mass alloc. coef. ⁴	0.00004	0.00004	n.a.	n.a.	n.a.	n.a.	–	/Helmisaari et al. 2002/
Frac. stem to coarse root	0.15	0.15	0.12	0.8	0.75	0	–	/Nordin et al. 1998, Johansson 2000, Helmisaari et al. 2002, Uri et al. 2002, Larcher 2003/
Litterfall (old biomass)								
Leaf (during dormancy) ⁵	cal.	0.055	0.1	0.1	0.1	0.1	day ⁻¹	Assumed
Stem	0.000018	0.000018	0.000018	0.00091	0.00091	0.1	day ⁻¹	Assumed
Coarse roots	0.000018	0.000018	0.000018	0.00091	0.00091	0.00091	day ⁻¹	Assumed
Fine root	0.0027	0.0027	0.0027	0.0027	0.0027	0.0027	day ⁻¹	Assumed

Property	Spruce	Pine	Alder	Blueberry	Cowberry	Grass/herb	Unit	Ref.
Min C/N ratio plants⁶								
Leaf	22	22	11	23	30	15	gC gN ⁻¹	/Ericsson 1994, Nilsson et al. 2001, Goverde et al. 2002/ (Nordin pers. comm.)
Stem and coarse roots	830	830	265	37	40	15	gC gN ⁻¹	/Ericsson 1994, Goverde et al. 2002/ (Nordin pers. comm., Olsson pers. comm.)
Fine root	40	40	18	64	69	40	gC gN ⁻¹	/Ericsson 1994, Persson and Nilsson 2001, Nordin and Näsholm 1997/ (Nordin pers. comm.)
Physical properties								
Leaf mass/unit leaf area	100	80	35	35	65	85	gC m ⁻²	/Bossel 1996, Middleton et al. 1997, Reich et al. 1998, Waring and Running 1998, Johansson 2000, Tsiatas et al. 2004, Foster and Brooks 2005/
Max height	30	20	16	0.3	0.2	0.8	m	(Tagesson unpublished data)
Root lowest depth	0.7	0.4	0.45	0.3	0.3	0.55	m	/Lindborg 2005/
Plant albedo	8	8	15	10	10	25	%	/Oke 1987, Betts and Ball 1997, Gustafsson et al. 2001/
Max. surface coverage	0.9	0.84	0.97	1	1	1	m ² m ⁻²	(Tagesson unpublished data)

cal. = calibrated; n.a. = not available. ¹Photosynthesis calculated as a linear function of absorbed radiation multiplied by response functions for leaf temperature and leaf C/N ratio.

²Growth respiration is deducted from gross photosynthesis before allocation to different storage organs of the plant and calculation on maintenance respiration. ³Same for coarse roots.

⁴Factor describing an increase in the allocation to roots with tree biomass. ⁵All plant types loose their leaves in the autumn at the onset of dormancy except spruce that looses its needles constantly over the season. ⁶Minimum C/N ratio measured in fertilisation experiments.

Table A2. Calibrated parameters, different ecosystems.

Property	Grassland	Alder	Pine	Spruce	Spruce managed	Unit
Plant						
Threshold C/N ratio leaf, Field ¹	144 ± 44	116 ± 19	123 ± 39	115 ± 33	123 ± 33	gC gN ⁻¹
Leaf allocation coef., Tree	n.a.	0.25 ± 0.06	0.24 ± 0.05	0.21 ± 0.06	0.18 ± 0.05	–
Root allocation coef., Tree	n.a.	0.17 ± 0.07	0.47 ± 0.05	0.47 ± 0.06	0.50 ± 0.05	–
Leaf allocation coef., Field	0.63 ± 0.12	0.55 ± 0.09	0.19 ± 0.08	0.21 ± 0.09	0.23 ± 0.06	–
Root allocation coef., Field	0.36 ± 0.04	0.45 ± 0.11	0.13 ± 0.05	0.10 ± 0.05	0.10 ± 0.04	–
Mobile allocation coef, Tree ²	n.a.	0.09 ± 0.06	0.16 ± 0.09	0.28 ± 0.12	0.32 ± 0.13	gC gC ⁻¹
Mobile allocation coef, Field ²	0.40 ± 0.21	0.96 ± 0.13	0.68 ± 0.32	0.48 ± 0.21	0.56 ± 0.22	gC gC ⁻¹
Maint. resp. leaf, Tree	n.a.	0.0051 ± 0.00093	0.0030 ± 0.0016	0.0038 ± 0.0012	0.0028 ± 0.0014	day ⁻¹
Maint. resp. stem, Tree ³	n.a.	0.00032 ± 0.00012	n.a.	n.a.	n.a.	day ⁻¹
Maint. resp. fine roots, Tree	n.a.	0.0058 ± 0.0027	n.a.	n.a.	n.a.	day ⁻¹
Maint. resp. leaf, Field ⁴	0.010 ± 0.0034	0.015 ± 0.0088	0.017 ± 0.011	0.025 ± 0.0049	0.0010 ± 0.0070	day ⁻¹
Maint. resp. stem, Field ^{3, 4}	0.0051 ± 0.0017	0.0076 ± 0.0044	0.0087 ± 0.0056	0.012 ± 0.0025	0.0049 ± 0.0035	day ⁻¹
Maint. resp fine roots, Field ⁴	0.0034 ± 0.0011	0.0051 ± 0.0029	0.0058 ± 0.0037	0.0083 ± 0.0017	0.0033 ± 0.0023	day ⁻¹
Leaf litterfall rate, Tree ⁵	n.a.	n.a.	n.a.	0.00049 ± 0.00025	0.00044 ± 0.00019	day ⁻¹
N fixation, Tree ⁶	n.a.	0.34 ± 0.23	n.a.	n.a.	n.a.	gN gN ⁻¹
Soil						
C/N ratio microbes ⁷	14 ± 2.3	12 ± 3.5	20 ± 2.9	19 ± 1.8	19 ± 2.9	gC gN ⁻¹
Decomposition rate humus	15.3 ± 3.4	20.7 ± 3.1	18.6 ± 3.9	18.6 ± 3.6	16.1 ± 3.2	day ⁻¹ ·10 ⁻⁵
Organic uptake rate litter ⁸	18.5 ± 5.7	13.5 ± 6.0	16.8 ± 6.2	20.4 ± 3.4	17.1 ± 5.5	day ⁻¹ ·10 ⁻⁵
Organic uptake rate humus ⁹	18.5 ± 5.7	13.5 ± 6.0	16.8 ± 6.2	20.4 ± 3.4	17.1 ± 5.5	day ⁻¹ ·10 ⁻⁷

¹Parameters allowed to vary according to literature values /Field and Mooney 1986, Thornley and Cannell 1992, Wikström and Ericsson 1995/. ²Plant retention of carbon at leaf abscission in relation to original carbon content in leaf. Fixed relationship between tree and plant according to Ericsson /Ericsson 1994/. ³Same for coarse roots. ⁴Maintenance respiration in the field layer is distributed between the different plant organs as: leaf = 3; stem = 1.5; root = 1 according to Penning de Vries /Penning de Vries 1975/. ⁵Constant over the whole season for Norway spruce, only after the onset of dormancy for pine and alder. ⁶Fraction of total N plant demand. ⁷The C/N ratio of microbes affects the mineralisation rate of nitrogen. ⁸The organic uptake of nitrogen represents the uptake of amino acids by mycorrhiza to the plant. ⁹Assumed to be a hundredth of the organic uptake from litter.

Table A3. Criteria of acceptance, different ecosystems. State and auxiliary variables.

Property	Grassland	Alder	Pine	Spruce	Unit	Ref.
State variables						
ΔC Soil	0 (-100/100)	0 (-100/100)	0 (-100/100)	0 (-100/100)	gC m ⁻² yr ⁻¹	Assumed
ΔC Tree	n.a.	0 (-50/50)	0 (-50/50)	0 (-50/50)	gC m ⁻² yr ⁻¹	Assumed
ΔC Field	0 (-20/20)	0 (-20/20)	0 (-20/20)	0 (-20/20)	gC m ⁻² yr ⁻¹	Assumed
C Soil	13,000 (11,000/15,000)	18,850 (14,000/23,000)	8,000 (7,000/16,000)	8,000 (7,000/16,000)	gC m ⁻²	/Blombäck 1998, Olsson 2000, Kutch et al. 2001b/
C Tree	n.a.	6,200 (4,000/9,000)	6,570 (3,000/7,000)	9,183 (9,000/9,400)	gC m ⁻²	/Johansson 2000, Helmisaari et al. 2002, Skogsdata 2003/
C Field	439 (250/630)	328 (5/660)	95 (60/130)	261 (90/420)	gC m ⁻²	/Löfgren 2005/
ΔN Ecosystem	0 (-5/5)	0 (-5/5)	0 (-5/5)	0 (-5/5)	gN m ⁻² yr ⁻¹	Assumed
<i>C distribution, Tree:</i>						
Leaf	n.a.	2 (0/12)	4 (0/14)	4 (0/14)	% of total	/Johansson 2000, Helmisaari et al. 2002, Uri et al. 2002/
Stem	n.a.	83 (73/93)	83 (73/93)	83 (73/93)	% of total	/Johansson 2000, Helmisaari et al. 2002, Uri et al. 2002/
Coarse roots	n.a.	11 (1/21)	11 (1/21)	11 (1/21)	% of total	/Johansson 2000, Helmisaari et al. 2002, Uri et al. 2002/
Fine roots	n.a.	4 (0/14)	2 (0/12)	2 (0/12)	% of total	/Johansson 2000, Helmisaari et al. 2002, Uri et al. 2002/
<i>C distribution, Field:</i>						
Leaf	55 (45/65)	55 (45/65)	15 (5/25)	20 (10/30)	% of total	/Nordin et al. 1998, Larcher 2003/
Stem	10 (0/20)	10 (0/20)	20 (10/30)	15 (5/25)	% of total	/Nordin et al. 1998, Larcher 2003/
Coarse roots	0	0	60 (50/70)	59 (49/69)	% of total	/Nordin et al. 1998, Larcher 2003/
Roots	35 (25/45)	35 (25/45)	5 (0/15)	6 (0/16)	% of total	/Nordin et al. 1998, Larcher 2003/
<i>Auxiliary variables</i>						
C/N ratio soil	18 (15/25)	17 (15/23)	20 (15/25)	20 (15/25)	gC gN ⁻¹	/Blombäck 1998, Dilly et al. 2000, Kutch et al. 2001a, Berggren et al. 2004/
N retention, Tree ¹	n.a.	0.25 (0/45)	0.15 (0.01/0.35)	0.4 (0.2/0.6)	gN gN ⁻¹	/Ericsson 1994/
N retention, Field ²	0.7 (0.5/0.9)	0.7 (0.5/0.9)	0.7 (0.5/0.9)	0.7 (0.5/0.9)	gN gN ⁻¹	/Ericsson 1995/
LAI Tree	n.a.	1.5 (0.5/8)	3.2 (2.2/4.2)	3.6 (2.6/4.6)	m ² m ⁻²	/Johansson 2000/ (Tagesson unpubl. data)
LAI Field	3 (0.5/4)	2 (1/3)	1 (0.5/2)	1 (0.5/2)	m ² m ⁻²	Assumed
<i>Max C/N ratio, Tree</i>						
Stem	n.a.	n.a.	n.a.	1,000 (0/1,500)	gC gN ⁻¹	/Johnson and Lindberg 1992/
Needles	n.a.	n.a.	n.a.	90 (0/100)	gC gN ⁻¹	/Johnson and Lindberg 1992/

¹ Retention of nitrogen at leaf abscission.

Table A4. Criteria of acceptance, different ecosystems. Flow variables.

Property	Grassland	Alder	Pine	Spruce	Unit	Ref.
Organic of tot. N uptake	0.1 (0.01/0.8)	0.1 (0.01/0.8)	0.1 (0.01/0.8)	0.1 (0.01/0.8)	gN gN ⁻¹	/Näsholm et al. 1998/
N fixation	n.a.	6 (4/8.5)	n.a.	n.a.	gN m ⁻² yr ⁻¹	/Dilly et al. 2000/
DOC leaching	n.a.	12.5 (-25%/+25%)	3.5 (-25%/+25%)	3.5 (-25%/+25%)	gC m ⁻² yr ⁻¹	/Canham et al. 2004/
Plant resp./tot. resp.	0.5 (0.3/0.7)	0.7 (0.6/0.8)	0.5 (0.3/0.7)	0.5 (0.3/0.7)	–	/Waring and Running 1998, Kutch et al. 2001b/
Heterotrophic/tot. soil resp.	0.70 (0.60/0.80)	0.35 (0.20/0.70)	0.25 (0.10/0.40)	0.25 (0.10/0.40)	–	/Dilly et al. 2000, Raich and Tufekcioglu 2000, Kutch et al. 2001b/
NPP/GPP	0.50 (0.40/0.60)	0.45 (0.35/0.60)	0.46 (0.25/0.60)	0.46 (0.25/0.60)	–	/Waring and Running 1998, Kutch et al. 2001b, Chapin et al. 2002/
NPP tree	n.a.	950 (400/1,300)	670 (-10%/+10%)	700 (200/1,200)	gC m ⁻² yr ⁻¹	/Helmisaari et al. 2002, Schultze et al. 2005/
NPP tree above ground	n.a.	400 (250/550)	n.a.	n.a.	gC m ⁻² yr ⁻¹	/Kutch et al. 2001b, Uri et al. 2002/
NPP field	222 (130/310)	40 (5/78)	25 (10/40)	12 (5/20)	gC m ⁻² yr ⁻¹	/Löfgren 2005/
<i>Distr. NPP Tree:</i>						
Leaf	n.a.	n.a.	14 (4/24%)	14 (4/24)	% of NPP tree	/Helmisaari et al. 2002/
Stem	n.a.	n.a.	18 (8/28)	18 (8/28)	% of NPP tree	/Helmisaari et al. 2002/
Coarse roots	n.a.	n.a.	8 (0/18)	8 (0/18)	% of NPP tree	/Helmisaari et al. 2002/
Fine roots	n.a.	n.a.	60 (50/70)	60 (50/70)	% of NPP tree	/Helmisaari et al. 2002/
<i>Litterfall Tree:</i>						
Leaf of above ground	n.a.	n.a.	0.70 (0.40/0.90)	0.70 (0.40/0.90)	–	/Waring and Running 1998/
Above ground	n.a.	129 (-10%/+10%)	n.a.	70 (60/100)	gC m ⁻² yr ⁻¹	/Berggren et al. 2004/
Leaf C	n.a.	n.a.	40 (-10%/10%)	n.a.	gC m ⁻² yr ⁻¹	/Flower-Ellis 1985/
Leaf N	n.a.	6 (-10%/10%)	n.a.	n.a.	gN m ⁻² yr ⁻¹	/Uri et al. 2002/
Below ground	n.a.	135 (-10%/+10%)	n.a.	445 (-10%/+10%)	gC m ⁻² yr ⁻¹	/Berggren et al. 2004/
<i>Litterfall Field:</i>						
Above ground	72 (-25%/+25%)	41 (-25%/+25%)	8 (-25%/+25%)	4 (-25%/+25%)	gC m ⁻² yr ⁻¹	/Löfgren 2005/
Below ground	150 (-25%/+25%)	84 (-25%/+25%)	17 (-25%/+25%)	8 (-25%/+25%)	gC m ⁻² yr ⁻¹	/Löfgren 2005/

Table A5. Criteria for acceptance spruce (managed). Only criteria different from spruce (natural).

Property	Values							Unit	Ref.
<i>C Tree f(age):</i>	7	16	26	36	51	71	91	yr	
<i>C Tree</i> ¹	0.64	1.32	3.52	5.66	7.47	8.93	9.79	kgC m ⁻²	/Marklund 1988, Skogsdata 2003, Swedish Environmental Protection Agency 2005/
<i>C Tree change f(age):</i>	12	21	31	44	61	81	99	yr	
ΔC Tree ¹	75	221	214	121	73	43	-30	gC m ⁻² yr ⁻¹	/Marklund 1988, Skogsdata 2003, Swedish Environmental Protection Agency 2005/
<i>C dist. Tree:</i>	15 years		35 years		100 years			yr	
Leaf	9		9		4			% of total	/Helmisaari et al. 2002/
Stem	66		69		83			% of total	/Helmisaari et al. 2002/
Coarse roots	10		15		11			% of total	/Helmisaari et al. 2002/
Fine roots	15		7		2			% of total	/Helmisaari et al. 2002/
<i>Distr. NPP Tree:</i>	15 years		35 years		100 years			yr	
Leaf	15		12		14			% of NPP tree	/Helmisaari et al. 2002/
Stem	39		26		18			% of NPP tree	/Helmisaari et al. 2002/
Coarse roots	3		3		8			% of NPP tree	/Helmisaari et al. 2002/
Fine roots	43		59		60			% of NPP tree	/Helmisaari et al. 2002/
<i>Litterfall Tree:</i>	<30 years			>30 years				yr	
Above ground	40			70				gC m ⁻² y ⁻¹	/Berggren et al. 2004/
Below ground	118			445				gC m ⁻² y ⁻¹	/Berggren et al. 2004/

¹Calculated from standing stock volume /Skogsdata 2003/ using expansion factors derived from Marklund /Marklund 1988/, according to the Swedish Environmental Protection Agency /Swedish Environmental Protection Agency 2005/.